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TABLE OF CONTENTS

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7101

KINDS AND ABUNDANCE OF FISH LARVAE IN THE EASTERN TROPICAL PACIFIC, BASED ON COLLECTIONS MADE ON EASTROPAC I

Elbert H. Ahlstrom[1]

ABSTRACT

This paper deals with kinds and counts of fish larvae obtained in 482 oblique plankton hauls taken over an extensive area of the eastern tropical Pacific on EASTROPAC I, a four-vessel cooperative survey made during February-March 1967. On the basis of abundance of larvae, the dominant fish group in oceanic waters are the myctophid lanternfishes (47 %), gonostomatid lightfishes (23 %), hatchetfishes, Sternoptychidae (6 %), bathylagid smelts (5 %). Scombrid larvae ranked fifth, and exceeded 2 % of the count.

Two kinds of larvae were outstandingly abundant: larvae of the lanternfish *Diogenichthys laternatus* made up over 25 % of the total, while larvae of the gonostomatid genus *Vinciguerria* made up almost 20 %. More fish larvae were obtained per haul, on the average, in the eastern tropical Pacific than were obtained per haul in the intensively surveyed waters of the California Current region off California and Baja California.

EASTROPAC I was the first and most wide-ranging of a series of cooperative cruises made in the eastern tropical Pacific between February 1967 and April 1968. A vast expanse of the eastern tropical Pacific was surveyed on EASTROPAC I, extending from lat 20° N to 20° S, and from the American coasts offshore to long 126° W (Fig. 1). Four research vessels participated in EASTROPAC I: *Alaminos* operated by Texas A & M, occupied the inner pattern, while *Rockaway* operated by the U.S. Coast Guard, *David Starr Jordan* operated by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service), and *Argo* operated by the Scripps Institution of Oceanography, occupied patterns successively seaward. The oceanographic, biological, and meteorological data collected on EASTROPAC cruises will be graphically presented in a series of EASTROPAC atlases, including generalized charts dealing with fish eggs and larvae.

The present paper is the result of a chain of events that began 2 decades ago, at the initiation of CalCOFI (California Cooperative Oceanic Fisheries Investigations) in which a large-scale sea program was set up to investigate the distribution and abundance of sardine spawning, and the factors underlying fluctuations in survival of the early life-history stages of sardines. The plankton collections not only contained eggs and larvae of sardine but those of most other pelagic fishes in the California Current region. A decision was made to attempt to identify and enumerate all fish larvae in the collections in order to obtain more precise information about the ecological associates of the sardine. At that time few fish larvae, other than those of the sardine and anchovy, could be identified.

Within a few years most kinds of fish larvae were identified to genus or species. Once the larvae were identified and enumerated, it became obvious that this was an exceptionally useful tool for evaluating fish resources. Most oceanic fishes have pelagic eggs and/or larvae that are distributed in or just below the photic zone, i.e. within the upper 150 to 200 m of depth. At no other time in their life histories are so many kinds of fishes associated together—deep-sea fishes (mesopelagic and bathypelagic) as well as epipelagic species—where they can be collected quantitatively with a single type of gear, a plankton net.

Once the larvae of the pelagic fish fauna of a region, such as those in the California Current region, are known, there is a large trans-

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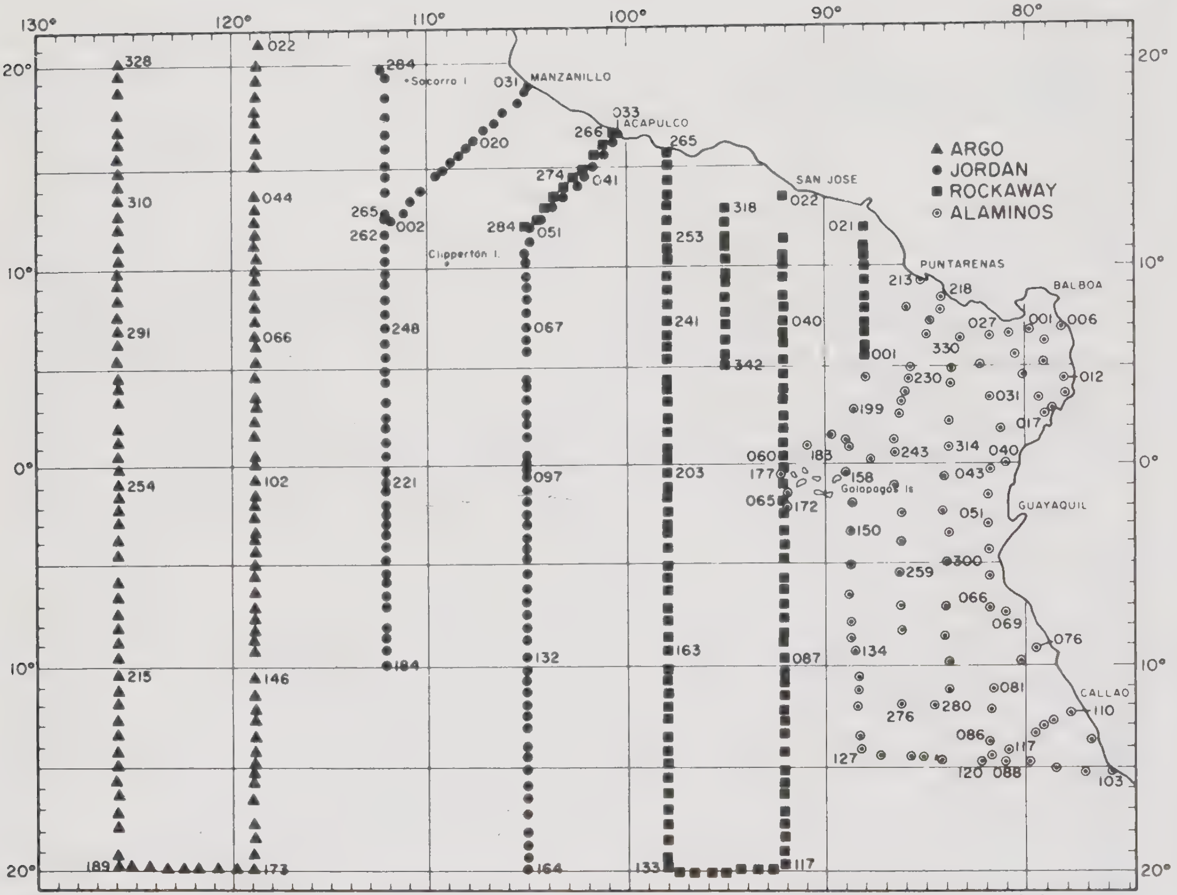
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⊙ ALAMINOS
MANZANILLO
ACAPULCO
SAN JOSE
PUNTARENAS
BALBOA
GUAYAQUIL
CALLAO
Socorro I.
Clipperton I.
Galapagos Is
328
310
291
254
215
189
022
044
066
102
146
173
284
265
262
248
221
184
031
020
002
266
274
041
284
051
067
097
132
164
033
265
253
241
203
163
133
318
342
022
040
060
177
065
172
087
117
021
001
213
218
027
330
001
006
230
012
199
031
017
188
243
314
040
158
043
150
051
259
300
066
069
134
076
081
280
276
110
086
117
127
120
088
103

FIGURE 1.—Location of plankton stations occupied by four research vessels participating in EASTROPAC I. Symbols for vessels indicated in legend above. Samples collected from *Argo* are numbered as 11.000 series (as 11.022, 11.173), samples from *David Starr Jordan* as 12.000 series, *Rockaway* samples as 13.000 series and *Alaminos* samples as 14.000 series.

ference of the accumulated knowledge and skills for work in other areas, such as, in this instance, the eastern tropical Pacific. My study was undertaken to demonstrate the value of identifying all elements of the fish fauna of tropical regions, rather than restricting interest to scombrid larvae. Much information can be gained for little extra expense (a few percent of the cost of collecting the material at sea). Of equal consequence, identification of all kinds of fish larvae can be made more critically including scombrid larvae.

METHODS OF MAKING ZOOPLANKTON COLLECTIONS

Three nets, differing in size and in coarseness of mesh, were employed to collect zooplankton and micronekton on EASTROPAC cruises. In this paper I am concerned primarily with oblique hauls made with the net of intermediate size and mesh—a net, 1-m mouth diameter, constructed of 505 μ nylon (Nitex) cloth, with approximately a 5 to 1 ratio of effective straining surface (pore area) to mouth area. This net was paired in an assembly frame with a finer-meshed net when hauled obliquely, but was used alone for taking surface hauls. The finer-meshed net was 0.5 m in diameter at the mouth, constructed of 333 μ Nitex cloth, with approximately an 8 to 1 ratio of effective straining surface to mouth area. The third net, used for collecting micronekton, had a 5-ft square mouth opening and was constructed of mesh measuring approximately 5.5 × 2.5 mm; this net could not be operated from the research vessel *Rockaway* on EASTROPAC I but was employed from the other three vessels.

Usually four zooplankton collections were made at each "biological" station: an oblique collection and a surface collection with the 1-m net, an oblique collection with the 0.5-m net, and an oblique collection with the micronekton net.

In taking oblique plankton hauls, the 1-m net was paired in an assembly frame with the 0.5 m net. The assembly of nets was fastened to the towing cable by a bridle about 5 m above a 100-lb weight. The assembly was lowered to depth by paying out 300 m of towing cable at the controlled rate of 50 m of wire per minute. The assembly remained at depth for 0.5 min and then was retrieved at a uniform rate of 20 m per min. Total towing time was about 21.5 min. Towing speed was ca. 2 knots. The depth reached by the net was estimated from the angle of stray (departure from the vertical) of the towing cable. We sought to maintain an angle of stray of 45°, which lowered the assembly to a depth of approximately 210 m. Our concern was to sample the upper 200-m stratum. The average depths of hauls taken by the four research vessels are summarized in Table 1. Over 80 % of the hauls made on EASTROPAC I were lowered to depths of 200 m or more, and nearly 95 % reached depths of 180 m or greater. However, two hauls were exceptionally shallow (71-90 m), and nine additional hauls were taken to depths of less than 150 m.

Usually four paired net-assembly hauls were taken per day, spaced at about 6-hr intervals. Although the four hauls were planned to be taken at about midnight, dawn, noon, and sunset, the timing of hauls was not coordinated between research vessels. The middle-of-the-night hauls were all taken before midnight (2201-2400) on *Rockaway*, for example, while on *Argo* most hauls were made after midnight (between 0001 and 0400 hr). The time of day of occupancy of stations (based on the midtime of each haul) is summarized by hourly intervals in Table 2. At least some hauls were taken during every hour of the day, although fewer than 10 (2-8) were obtained during six of the hourly intervals. Fewest hauls were obtained between 0901 and 1000 hr (2 hauls) and between 2101 and 2200 hr (4 hauls), whereas the largest number of hauls were taken between 2201 and 2300 hr (59 hauls) and between 1001 and 1100 hr (53 hauls). Hauls were made with equal frequency during the four periods of the day on *Argo*, *Jordan*, and *Rockaway*; most plankton hauls were taken near midnight or noon from *Alaminos*.

TABLE 1.—Depth of paired oblique plankton hauls taken by the four research vessels on EASTROPAC I. (Net lowered by paying out 300 m of towing cable)

Average depth of haul	Number of hauls taken to each depth interval from				
	Argo	*David Starr Jordan*	*Rockaway*	*Alaminos*	All vessels
M					
70.1- 80.0	--	--	--	1	1
80.1- 90.0	--	--	--	1	1
90.1-100.0	--	--	--	--	--
100.1-110.0	--	--	--	1	1
110.1-120.0	--	--	--	--	--
120.1-130.0	2	--	--	3	5
130.1-140.0	1	--	--	1	2
140.1-150.0	--	1	--	--	1
150.1-160.0	--	--	1	2	3
160.1-170.0	2	--	2	2	6
170.1-180.0	2	2	2	1	7
180.1-190.0	15	5	4	5	29
190.1-200.0	21	10	11	10	52
200.1-210.0	41	59	58	30	188
210.1-220.0	26	44	57	41	168
220.1-230.0	9	--	3	5	17
230.1-240.0	--	--	1	--	1
Total	119	121	139	103	482

The numbering system for observations employed on EASTROPAC cruises made use of five digits divided into two groups, as 11.022, 12.002, etc. The outer digit preceding the period is the cruise number common to all vessels participating in a given EASTROPAC cruise; for EASTROPAC I, this number is 1. The other digit preceding the period is the identifying number given to each research vessel, with the lowest

TABLE 2.—Hour of day that paired oblique plankton hauls were taken from the four research vessels participating in EASTROPAC I. (Midtime of haul used.)

Hours of day	Number of hauls taken during each hour of the day from				
	Argo	*David Starr Jordan*	*Rockaway*	*Alaminos*	All vessels
0001-0100	7	10	0	3	20
0101-0200	8	7	0	2	17
0201-0300	5	2	0	0	7
0301-0400	9	0	7	0	16
0401-0500	1	1	17	1	20
0501-0600	2	9	10	3	24
0601-0700	7	10	1	1	19
0701-0800	13	10	0	0	23
0801-0900	7	0	0	0	7
0901-1000	0	0	0	2	2
1001-1100	1	0	26	26	53
1101-1200	1	5	5	10	21
1201-1300	7	22	3	1	33
1301-1400	12	3	1	4	20
1401-1500	8	0	0	0	8
1501-1600	1	1	12	1	15
1601-1700	0	0	10	3	13
1701-1800	8	6	12	6	32
1801-1900	7	19	1	0	27
1901-2000	10	1	0	0	11
2001-2100	3	3	0	0	6
2101-2200	0	1	0	3	4
2201-2300	2	2	23	32	59
2301-2400	0	9	11	5	25
Total	119	121	139	103	482

number given to the offshore vessel. The three digits following the period are numbers given to observations made from each vessel during a cruise, numbered sequentially. Not all "stations" included oblique plankton hauls; hence there are gaps in numbers applied to plankton collections.

The locations of plankton stations occupied by the four research vessels participating in EASTROPAC I are shown in Figure 1. Samples collected from the *Argo* are designated as the 11.000 series, samples from the *David Starr Jordan* as 12.000 series, *Rockaway* samples as 13.000 series and *Alaminos* samples as 14.000 series. In tables to follow, the series of samples taken by each vessel is designated by the above identifying series numbers. The aggregate of stations occupied by each vessel is referred to in text discussions as its pattern.

PROCESSING SAMPLES ASHORE

As noted above, only samples from 1-m oblique net hauls were sorted routinely for fish eggs and larvae. As a rule the entire sample was sorted; in fact only six collections out of 482 were aliquoted — four collections were split into 50 % aliquots, two collections into 25 % aliquots.

The author made all identifications and counts of larvae from EASTROPAC I collections. Actual counts of larvae rather than standardized values (see below) are used in tabulation throughout this paper, except one (Table 7). There are several reasons why I chose to do this. As indicated previously, all hauls were made in a roughly comparable fashion. In many studies the investigator is interested in the presence or absence of the larvae of a given species or assemblage of species as such relate to water masses, community composition, time of day, etc. Such information is most readily obtained from records of actual counts. Some statistical tests require the use of original counts rather than standardized data. For persons interested in deriving standardized counts comparable with those employed for CalCOFI data (Ahlstrom, 1953), standard haul factors for the 482 oblique hauls taken with the 1-m net on EASTROPAC I are given in Appendix Table 7.

Two major considerations in the quantitative sampling of fish larvae for resources evaluation are (1) how well has their depth range been covered and (2) how effectively have the larvae been sampled within this layer?

We do not have direct answers to either of these questions from EASTROPAC cruises. No studies were made on depth distributions of fish eggs and larvae in the EASTROPAC area. As will appear, fewer fish larvae were obtained during daylight hours than in night hauls; however, we lack information on how completely larvae were sampled in night hauls.

DEPTH DISTRIBUTION OF FISH LARVAE

Although collecting methods used on EASTROPAC did not permit a study of depth distribution of fish larvae, such information for the California Current region off California and Baja California and in a less detailed way for the NORPAC Expedition of 1955 are available (Ahlstrom, 1959).

In the California Current region, most fish eggs and larvae were distributed within the upper mixed layer or in the upper portion of the thermocline, between the surface and approximately 125 m. Of the 15 most common kinds of fish larvae taken in vertical distribution series, 12 were so distributed (ibid., p. 134). Two of the kinds that occurred most commonly below the thermocline were bathylagid smelts, closely related to the two common bathylagid smelts taken on EASTROPAC I.

On the NORPAC Expedition of August 1955, two depth strata were sampled at most stations; a closing net, fastened to the towing cable 200 m below a standard open plankton net, sampled the level between 262 and 131 m on the average, while the upper net sampled from the surface to approximately 131 m deep. Only about one-ninth as many larvae were taken in the closing net hauls as in the upper net hauls; fully half of these were larvae of hatchetfish, family Sternoptychidae, largely absent from upper net hauls. The two most abundant kinds of fish larvae taken on EASTROPAC I were those of the myctophid lanternfish, *Diogenichthys laternatus,* and of the gonostomatid lightfish, *Vinciguerria* spp. In NORPAC collections, only 3 % of the larvae of *D. laternatus* were taken in the closing net hauls and only 2 % of the *Vinciguerria* larvae. Among the kinds of larvae common to both the NORPAC and EASTROPAC surveys that occurred in significant numbers in the deeper NORPAC collections were those of *Chauliodus* (72 % taken in closing net hauls), *Protomyctophum* (48 %) and *Idiacanthus* (32 %).

Inasmuch as the vertical distribution studies in the California Current region had pointed up the importance of the thermocline in the depth distribution of larvae, the pattern of thermocline depth was analyzed for EASTROPAC I (Table 3).

Thermocline depth was invariably shallow in the inner pattern occupied by *Alaminos* (data not included in Table 3); the greatest depth recorded was only 40 m, and the majority of observations were at depths shallower than 20 m. Along the six station lines covered in Table 3, thermocline depths were shallowest near the equator, and usually were deepest at the northern (20-15° N) and southern (15-20° S) ends of the lines. The thermocline also deepened offshore; approximately three-fourths of the records of thermocline depths of 50 m or greater were from the two outer lines, occupied by *Argo.*

Most oblique plankton hauls taken on EASTROPAC I sampled to depths of 200 m or more (Table 2), hence sampled considerably deeper than the thermocline in all parts of the EASTROPAC area.

EFFECTIVENESS OF SAMPLING FISH LARVAE IN DAYLIGHT HAULS AS COMPARED WITH NIGHT HAULS

Fewer fish larvae were obtained in hauls made during daylight hours than at night (Table 4). Original (unstandardized) counts of larvae averaged 2.76 times as many in night hauls as in day hauls, 285 larvae per occupancy as compared with 103 larvae. Hauls made within 1 hr of sunrise or sunset contained intermediate numbers of larvae, averaging 217 larvae per occupancy.

TABLE 3.—Summary of records of thermocline depths along six station lines occupied by the research vessels *Rockaway, David Starr Jordan,* and *Argo* on EASTROPAC I.

Station line along longitude	Range in depth of thermocline (*m*) at latitudes								All latitudes
	20-15° N	15-10° N	10-5° N	5° N-0°	0-5° S	5-10° S	10-15° S	15-20° S	
92° W	--	0-15	7-14	5-29	0-16	15-40	24-45	30-54	0-54
98°	16-30	13-68	23-44	5-13	2-27	13-32	20-48	40-60	2-68
105°	--	37-50	27-44	0-20	0-28	23-45	26-55	54-66	0-66
112°	8-42	41-79	32-58	0-37	2-22	33-52	--	--	0-79
119°	36-67	44-90	42-55	0-85	0-65	34-76	50-73	30-71	0-90
126°	52-116	45-79	35-49	0-42	0-60	40-71	43-71	43-70	0-116
% obs. with T. D. shallower than 10.1 m	17 %	8 %	7 %	46 %	43 %	0	0	0	20 %
% obs. with T. D. deeper than 49.9 m	56 %	46 %	9 %	11 %	9 %	25 %	35 %	63 %	26 %

TABLE 4.—Occurrence (positive hauls) and abundance (original counts) of fish larvae in day hauls as compared with night hauls and with hauls taken within 1 hr of sunrise or sunset, summarized by family and vessel pattern.

Vessel pattern and family	Day hauls			Night hauls				Hauls within ± 1 hr of sunrise or sunset			Total hauls		
	Number positive hauls	Total larvae	Average number per occupancy (D)	Number positive hauls	Total larvae	Average number per occupancy (N)	$\overline{N}/\overline{D}$	Number positive hauls	Total larvae	Average number per occupancy	Number positive hauls	Total larvae	Average number per occupancy
11.000 series													
Argo	(44)[1]			(42)				(33)			(119)		
Myctophidae	43	1,129	25.7	42	4,412	105.0	4.09	33	1,452	44.0	118	6,993	58.8
Gonostomatidae	44	727	16.5	42	2,619	62.4	3.78	32	1,317	39.9	118	4,663	39.2
Sternoptychidae	36	327	7.4	33	343	8.2	1.10	21	253	7.7	90	923	7.8
Bathylagidae	15	96	2.2	21	103	2.4	1.12	13	85	2.6	49	284	2.4
Melamphaidae	26	65	1.5	23	65	1.6	1.05	17	35	1.1	66	165	1.4
Scombridae	5	21	0.5	13	29	0.7	1.44	8	187	5.7	26	237	2.0
All others	42	687	15.6	42	1,012	24.1	1.54	32	555	16.8	116	2,254	18.9
Total	44	3,052	69.4	42	8,583	204.4	2.95	33	3,884	117.8	119	15,519	130.5
12.000 series													
Jordan	(34)			(37)				(50)			(121)		
Myctophidae	34	1,257	37.0	37	5,389	145.6	3.94	50	4,628	92.6	121	11,274	93.2
Gonostomatidae	32	451	13.3	37	2,417	65.3	4.91	49	1,914	38.1	118	4,782	39.5
Sternoptychidae	22	452	13.3	21	503	13.6	1.02	31	757	15.1	74	1,712	14.1
Bathylagidae	20	105	3.1	20	168	4.5	1.45	33	223	4.5	73	496	4.1
Melamphaidae	21	43	1.3	28	58	1.6	1.25	28	70	1.4	77	171	1.4
Scombridae	9	80	2.4	16	129	3.5	1.49	19	133	2.7	44	342	2.8
All others	34	766	22.5	37	2,009	56.8	2.52	49	1,244	24.9	120	4,109	34.0
Total	34	3,154	92.9	37	10,763	290.9	3.13	50	8,969	179.5	121	22,886	189.1
13.000 series													
Rockaway	(65)			(59)				(15)			(139)		
Myctophidae	65	3,761	57.9	58	8,557	145.0	2.50	14	2,911	194.1	137	15,229	109.6
Gonostomatidae	62	1,138	17.5	59	5,608	95.0	5.43	14	1,383	92.2	135	8,129	58.5
Sternoptychidae	47	798	12.3	45	829	14.1	1.14	14	534	35.6	106	2,161	15.5
Bathylagidae	43	475	7.3	37	411	7.0	0.95	13	189	12.6	93	1,075	7.7
Melamphaidae	42	130	2.0	43	132	2.2	1.12	11	59	3.9	96	321	2.3
Scombridae	30	131	2.0	29	435	7.4	3.65	10	39	2.6	69	605	4.4
All others	62	1,009	15.5	59	2,422	41.1	2.65	15	429	28.6	136	3,860	27.8
Total	65	7,442	114.5	59	18,394	311.8	2.72	15	5,544	369.6	139	31,380	225.8
14.000 series													
Alaminos	(50)			(46)				(7)			(103)		
Myctophidae	46	2,523	50.5	43	6,640	144.3	2.86	7	2,254	322.0	96	11,417	110.8
Gonostomatidae	41	874	17.5	41	2,550	55.4	3.17	6	1,048	149.7	88	4,472	43.4
Sternoptychidae	31	312	6.2	31	565	12.3	1.97	5	14	2.0	67	891	8.7
Bathylagidae	40	1,015	20.3	43	1,809	39.3	1.94	6	201	28.7	89	3,025	29.4
Melamphaidae	28	69	1.4	26	104	2.3	1.64	5	27	3.9	59	200	1.9
Scombridae	16	65	1.3	25	448	9.7	7.49	5	222	31.7	46	735	7.2
All others	45	1,406	28.1	45	2,557	55.6	1.98	6	621	88.7	96	4,584	44.5
Total	46	6,264	125.3	46	14,673	318.9	2.55	7	4,387	626.7	99	25,324	245.9
Complete EASTROPAC I	(193)			(184)				(105)			(482)		
Myctophidae	188	8,670	44.9	180	24,998	135.9	3.03	104	11,245	107.1	472	44,913	93.2
Gonostomatidae	179	3,190	16.5	179	13,194	71.7	4.35	101	5,662	53.9	459	22,046	45.7
Sternoptychidae	136	1,889	9.8	140	2,240	12.2	1.24	71	1,558	14.8	337	5,687	11.8
Bathylagidae	118	1,691	8.8	121	2,491	13.5	1.54	65	698	6.7	304	4,880	10.1
Melamphaidae	117	307	1.6	120	359	1.9	1.23	61	191	1.8	298	857	1.8
Scombridae	60	297	1.5	83	1,041	5.7	3.68	42	581	5.5	185	1,919	4.0
All others	183	3,868	20.0	183	8,090	44.0	2.20	102	2,849	27.2	468	14,807	30.7
Total	189	19,912	103.1	184	52,413	284.9	2.76	105	22,784	217.0	478	95,109	197.3

[1] Total number of hauls.

Larvae of some families of fishes were sampled almost as well in day hauls as in night hauls —including Sternoptychidae, Bathylagidae, and Melamphaidae. In contrast, less than one-fourth as many gonostomatid larvae and one-third as many myctophid larvae were taken in day hauls, on the average, as in night hauls. Catches of scombrid larvae were more variable with regard to time of sampling—the night-day ratio in the outer half of the EASTROPAC area was only about 1.5 to 1, whereas the ratio jumped to about 7.5 to 1 in the inner pattern occupied by *Alaminos*. Larvae collected about in equal amounts in day and night hauls were those known to occur principally below the thermocline.

Despite the lower abundance of larvae in day hauls as compared with night hauls, the percentage of hauls containing larvae of most families was only slightly lower (Table 5). The most marked day/night difference in frequency of occurrence was for scombrid larvae, these were taken in 45 % of night hauls, but in only 31 % of day hauls. In the discussions that follow I make use of all collection data, irrespective of time of collection.

TABLE 5.—Percentage of hauls containing larvae of the more abundant fish families on EASTROPAC I, grouped by day, night and dawn or sunset.

Family	Day hauls	Night hauls	Dawn or sunset hauls (± 1 hr)	All hauls
	%	%	%	%
Myctophidae	97.4	97.8	99.0	97.9
Gonostomatidae	92.7	97.3	95.2	95.0
Sternoptychidae	70.5	76.1	67.6	69.9
Bathylagidae	61.1	65.2	61.9	62.9
Melamphaidae	60.6	65.2	58.1	61.8
Scombridae	31.1	45.1	40.0	38.4
All others	94.8	99.5	97.1	97.1
Total	97.9	100.0	100.0	99.2

NUMBERS OF FISH LARVAE OBTAINED ON EASTROPAC I

Fish larvae were obtained in 478 of 482 oblique plankton tows made with the 1-m plankton net on EASTROPAC I. The number of larvae per collection ranged from 0 to 2,197, averaging 197 larvae (actual counts).

Differences in abundance of larvae with latitude are summarized for the four series in Table 6. Fish larvae were obtained in largest numbers, on the average, in an equatorial band extending from about lat 10° N to 5° S. The least productive waters for fish larvae were in the central water mass of the South Pacific, especially between lat 15° and 20° S.

Abundance of fish larvae also decreased offshore, averaging only 130 larvae per haul in the outer pattern, occupied by *Argo*, as compared with 246 larvae per haul in the inner pattern, occupied by *Alaminos*.

Tropical waters and oceanic waters are usually considered to be relatively unproductive, compared with temperate coastal regions such as the California Current region (Ryther, 1969). Hence, it is surprising to find that the average number of fish larvae obtained per haul on EASTROPAC I was larger than either on the CalCOFI cruises from the California Current region (Ahlstrom, 1969) or on NORPAC (un-

TABLE 6.—Total catches of fish larvae (actual counts) taken by the four research vessels on EASTROPAC I, summarized by latitude.

Latitude	*Argo* 11.000 Series		*David Starr Jordan* 12.000 Series		*Rockaway* 13.000 Series		*Alaminos* 14.000 Series		Total EASTROPAC I		
	No. hauls	No. larvae	No. hauls	No. larvae	No. hauls	No. larvae	No. hauls	No. larvae	No. hauls	No. larvae	Average no. larvae per haul
20° N-15° N	16	1,070	20	4,128	5	462	--	--	41	5,660	138.0
15° N-10° N	14	1,372	23	3,130	26	5,508	--	--	63	10,010	158.0
10° N- 5° N	14	2,516	14	3,344	29	10,104	15	5,167	72	21,131	293.5
5° N- 0°	14	4,797	15	4,403	14	4,331	27	11,329	70	24,860	355.1
0° - 5° S	14	2,089	18	5,454	14	4,350	17	5,042	63	16,935	268.8
5° S-10° S	13	1,370	15	1,051	14	2,360	16	2,113	58	6,894	118.9
10° S-15° S	14	1,512	8	863	15	2,337	28	1,673	65	6,385	98.2
15° S-20° S	20	793	8	513	22	1,928	--	--	50	3,234	64.7
Total	119	15,519	121	22,886	139	31,380	103	25,324	482	95,109	197.3

published data). Standard haul totals of larvae are used in this comparison (Table 7) not original counts. CalCOFI cruises repeatedly surveyed a coastal area extending 200 to 300 miles offshore between San Francisco, California, and Magdalena Bay, Baja California. NORPAC was the first comprehensive survey of the North Pacific, made in August-September 1955; the area surveyed by four CalCOFI vessels participating in NORPAC was between lat 20° and 45° N and offshore to long 150° W.

TABLE 7.—Comparison of the average number of fish larvae obtained per haul (standard haul values) EASTROPAC I, NORPAC, and CalCOFI cruises.

Cruises	Year	Number hauls	Average depth of hauls	Total number of fish larvae[1]	Average number larvae/haul
EASTROPAC I	1967	482	ca. 200 m	274,131	569
NORPAC	1955	196	ca. 260 m	27,000	[2]138
CalCOFI cruises	1956	1,407	ca. 140 m	408,140	290
	1957	1,493	ca. 140 m	493,550	331
	1958	1,852	ca. 140 m	456,020	246
	1959	2,182	ca. 140 m	470,450	216
	1960	1,826	ca. 140 m	504,980	277

[1] Standard haul totals.

[2] Data from two net hauls combined: an average of 124 larvae per haul were taken in upper net hauls (0 to 130 m) and an average of 14 larvae per haul in closing net hauls, sampling between ca. 260 and 130 m.

EASTROPAC hauls sampled a somewhat deeper stratum than hauls made on CalCOFI cruises, ca. 200 m as compared to ca. 140 m. As indicated previously, information is available for the majority of NORPAC stations on the relative abundance of fish larvae in the level between ca. 130 and 260 m (closing net hauls) as compared with the level above, 0 to 130 m. Only about one-ninth as many larvae were taken in the deeper hauls.

The difference between catches of larvae on EASTROPAC I and NORPAC are particularly marked—four times as many larvae were taken per haul, on the average, on EASTROPAC I as on NORPAC (both nets combined). For comparison with shallower CalCOFI hauls, I am assuming that 10 % of the EASTROPAC larvae were obtained in the level between ca. 140 and 200 m. The adjusted value for EASTROPAC larvae, 512 larvae per haul, on the average, is 1.55 times as large as the highest CalCOFI value listed (331 larvae per haul in 1957) and 2.35 times as large as the lowest value (216 larvae per haul in 1959).

The majority of EASTROPAC larvae were those of fishes which never attain a large size as adults—myctophids, gonostomatids, sternoptychids, etc.—hence numbers of larvae, per se, cannot be considered reliable indices of biomass. The familial composition of larvae was not dissimilar on NORPAC and EASTROPAC, however; hence this comparison of relative abundance of larvae is more relevant, as regards biomass, than the comparison with CalCOFI fauna.

KINDS OF FISH LARVAE OBTAINED ON EASTROPAC I

The kinds of larvae obtained on EASTROPAC I are summarized by family and vessel pattern in Table 8, the principal summary table in this paper. Larvae of more than 50 families are listed, but larvae of 10 families contributed 90 % of the total. The myctophids were the dominant group with 47.2 % of the larvae occurring in nearly 98 % of the collections. Gonostomatid larvae were about half as numerous, contributing 23.2 % of the larvae while occurring in 95 % of the collections. Hatchetfish larvae (Sternoptychidae) ranked third in abundance with 6 % of the larvae taken in 70 % of the hauls. Bathylagid larvae also exceeded 5 % of the total and occurred in 63 % of the collections. Scombrid larvae ranked fifth and exceeded 2 % of the count, followed by Bregmacerotidae, 1.9 %, Paralepididae, 1.7 %, Idiacanthidae, 1.0 %, Nomeidae, 1.0 %, and Melamphaidae, 0.9 %. About one-third of the remaining larvae were too poorly preserved (disintegrated) to identity.

On the basis of larval abundance, the dominant orders of fishes in oceanic waters are the Myctophiformes and Salmoniformes, making up between 85 and 88 %; the latter value assumes a proportionate representation of larvae of these groups in the "disintegrated" category, i.e., larvae too damaged or disintegrated to identify with certainty. Despite the dominance of fishes of the above two orders, a number of other groups of fishes are represented in the oceanic pelagic fish fauna. The berycoid fishes are rep-

TABLE 8.—Occurrences and counts of fish larvae taken in oblique 1.0-m plankton hauls on EASTROPAC I, summarized by family or larger grouping and by research vessel.

Family or larger grouping	Basic station data contained in Appendix Table no.		*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I	
	By family or larger grouping	By genus or species	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
[1]*1 Clupeidae	4		0	0	1	1	3	5	6	75	10	81
*2 Engraulidae	4		0	0	1	2	2	20	7	183	10	205
*3 Argentinidae		3	8	12	22	54	11	19	2	2	43	87
*4 Bathylagidae	1	3	49	284	73	496	93	1,075	89	3,025	304	4,880
*5 Gonostomatidae	1	3	118	4,663	118	4,782	135	8,129	88	4,472	459	22,046
*6 Sternoptychidae	1		90	923	74	1,712	106	2,161	67	891	337	5,687
*7 Astronesthidae	1		5	6	4	4	1	1	2	2	12	13
*8 Chauliodontidae	1		19	37	23	75	20	30	18	23	80	165
*9 Idiacanthidae	1		42	147	46	395	46	311	33	107	167	960
*10 Other Stomiatoidei	1	3	41	77	58	155	60	170	44	100	203	502
*11 Synodontidae	4		0	0	1	1	2	2	7	38	10	41
*12 Chlorophthalmidae			0	0	0	0	1	4	0	0	1	4
*13 Myctophidae	1	2	118	6,993	121	11,274	137	15,229	96	11,417	472	44,913
*14 Paralepididae	1	3	67	242	97	558	82	523	44	325	290	1,648
*15 Evermannellidae	3		14	20	4	6	9	12	0	0	27	38
*16 Scopelarchidae	1		35	64	46	104	39	120	22	41	142	329
*17 Scopelosauridae		3	2	2	3	3	1	1	3	10	9	16
18 Other Myctophiformes			7	8	2	2	1	2	2	2	12	14
19 Giganturidae			1	1	0	0	0	0	0	0	1	1
*20 Eel leptocephali	1		19	46	15	22	23	38	30	73	87	179
*21 Melamphaidae	1		66	165	77	171	96	321	59	200	298	857
22 Holocentridae			0	0	0	0	3	4	1	1	4	5
*23 Bregmacerotidae	1		62	291	56	825	56	435	21	254	195	1,805
24 Macrouridae			0	0	0	0	1	1	2	2	3	3
25 Scomberesocidae			0	0	0	0	1	1	0	0	1	1
*26 Exocoetidae	1	3	9	15	26	65	28	75	15	34	78	189
27 Trachypteridae	3		13	13	14	16	8	8	10	10	45	47
*28 Gempylidae-Trichiuridae	1	5	19	26	18	28	31	103	35	74	103	231
*29 Scombridae	1	3	26	237	44	342	69	605	46	735	185	1,919
*30 Istiophoridae			2	2	0	0	0	0	0	0	2	2
31 Ammodytidae			0	0	0	0	3	4	4	4	7	8
*32 Apogonidae		3	35	115	15	64	9	23	2	2	61	204
33 Balistidae			0	0	0	0	1	1	1	2	2	3
34 Bramidae	1		28	46	9	10	13	14	9	11	59	81
35 Callionymidae			0	0	0	0	0	0	8	12	8	12
*36 Carangidae	4	3	1	1	7	12	4	84	19	86	31	183
37 Carapidae			0	0	0	0	1	1	2	2	3	3
38 Champsodontidae			5	6	0	0	0	0	0	0	5	6
39 Chiasmodontidae	1		15	43	11	28	20	40	18	30	64	141
*40 Coryphaenidae		3	24	29	23	36	19	25	20	28	86	118
41 Gobiidae	4		0	0	7	17	23	262	30	251	60	530
42 Labridae	4		0	0	3	4	6	8	19	28	28	40
43 Mugilidae			0	0	0	0	0	0	5	9	5	9
*44 Nomeidae	1		39	178	52	346	51	291	36	146	178	961
45 Ophidiidae			1	1	1	1	0	0	4	18	6	20
46 Polynemidae			0	0	0	0	2	3	3	8	5	11
47 Sciaenidae			0	0	1	6	2	4	1	2	4	12
48 Scorpaenidae	4		1	1	5	8	15	41	27	113	48	163
49 Serranidae	4		0	0	3	15	3	53	20	184	26	252
50 Sphyraenidae			0	0	0	0	2	2	1	1	3	3
*51 Tetragonuridae		3	4	5	0	0	2	2	0	0	6	7
52 Triglidae			0	0	0	0	2	4	4	19	6	23
53 Uranoscopidae			0	0	0	0	0	0	1	1	1	1
*54 Bothidae		6	0	0	3	14	24	106	29	79	56	199
*55 Cynoglossidae		6	0	0	5	17	21	102	37	185	63	304
56 Lophiiformes	3		31	48	34	55	37	69	38	95	140	267
57 Other, including unidentified	1		69	257	56	323	54	436	57	523	236	1,539
58 Disintegrated larvae	1		89	515	97	837	90	400	73	1,389	348	3,141
Total			119	15,519	121	22,886	139	31,380	[2]99	25,324	[2]478	95,109

[1] Categories preceded by an asterisk are discussed in the text.

[2] No fish larvae were taken in four hauls of 14.000 series, hence total number of oblique 1.0-m collections was 482.

resented by Melamphaidae, a family of fishes that is almost as ubiquitous as the myctophids or gonostomatids. Fishes of the gadoid family, Bregmacerotidae, also are widely distributed in the warmer waters of all oceans. Among the ubiquitous epipelagics are the flyingfishes, Exocoetidae.

Only a moderate number of perciform fishes are widely distributed in offshore, oceanic waters. Among the more important are fishes of the families Scombridae, Gempylidae, Trichiuridae, Istiophoridae, Coryphaenidae, Bramidae, Nomeidae, Apogonidae, Chiasmodontidae, and Tetragonuridae.

Larvae of some demersal fishes have a much wider offshore distribution than one would associate with the known distribution of adults. Included in this group are larvae of bothid and cynoglossid flatfishes, and larvae of Scorpaenidae, Gobiidae, and Labridae.

Another widely distributed group in oceanic waters are the bizarre ceratioid fishes. The rotund larvae of these fishes were taken in about 30 % of the EASTROPAC collections, always in small numbers.

The basic data on the kinds and numbers of fish larvae obtained in the 482 EASTROPAC I collections are contained in six appendix tables, whose contents are summarized below, and keyed to Table 8 and to other tables in this report.

> Appendix Table 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I. This table contains 22 categories, mostly families, but for completeness, a category is included for "other identified larvae," one for "unidentified larvae" and one for "disintegrated larvae" (i.e., larvae too damaged or disintegrated to identify with any certainty).
>
> Appendix Table 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. Myctophid larvae are tabulated by species for 12 kinds, and by genus for 8 kinds. Also included are categories for unidentified myctophids, and total myctophids. A summary of this appendix table is contained in Table 15.
>
> Appendix Table 3.—Counts of selected categories of fish larvae by station. Table contains 23 categories including 10 species, 10 genera, 2 families, and 1 suborder; 9 of these were included in the category "other identified larvae" in Appendix Table 1.
>
> Appendix Table 4.—Summary of occurrences and numbers of larvae of eight families limited in distribution to a broad coastal band or around offshore islands. Only positive stations are included. These eight families also were included in the category "other identified larvae" in Appendix Table 1.
>
> Appendix Table 5.—Numbers and kinds of larvae of Gempylidae-Trichiuridae obtained in EASTROPAC I collections. Only positive stations are included. A summary of this appendix table is given in Table 19.
>
> Appendix Table 6.—Numbers and kinds of flatfish (Pleuronectiformes) larvae obtained in EASTROPAC I collections. Only positive hauls are included. A summary of this appendix table is given in Table 22.
>
> Appendix Table 7.—Standardized haul factors for the 482 oblique 1-m net hauls taken on EASTROPAC I. These factors adjust original counts of larvae to the comparable standard of numbers of larvae in 10 m^3 of water strained per meter of depth fished.

I will not attempt to comment on all 58 categories (family or larger grouping) summarized in Table 8, but will limit my discussion to 31 of these. In order to tie the text discussion closely to this table, I retain the numbers for categories as given in Table 8; those discussed in the text are preceded by an asterisk in this table.

COMMENTS ON LARVAE OF THE MAJOR FISH FAMILIES COLLECTED ON EASTROPAC I

1. CLUPEIDAE

(10 occurrences, 81 larvae)

Three species of clupeid larvae were taken in EASTROPAC I collections—*Opisthonema* sp.

(5 occurrences, 12 larvae), *Etrumeus acuminatus* Gilbert (2 occurrences, 6 larvae), and *Sardinops sagax* (Jenyns) (3 occurrences, 63 larvae). The latter two species were collected in the vicinity of the Galápagos Islands.

2. ENGRAULIDAE
(10 occurrences, 205 larvae)

The majority of the engraulids (5 occurrences, 174 specimens) were those of the Peruvian anchovy, *Engraulis ringens* Jenyns, collected at coastal stations between lat 6° and 13.5° S. Although larvae from only a few surface hauls have been sorted as yet, one haul was outstanding: the surface tow taken at station 14.069 contained 10,466 larvae and transforming specimens of Peruvian anchovy, *E. ringens*. Specimens ranged in size from 3.5 to 37.5 mm; most were between 4.0 and 7.5 mm in length but even transforming specimens, 20.0 to 37.5 mm long, were rather common (83 individuals). In the oblique 1-m haul at this station, 97 anchovy larvae were obtained.

3. ARGENTINIDAE
(43 occurrences, 87 larvae)

Three kinds of argentinid larvae were obtained: *Argentina* sp. (1 specimen), *Nansenia* sp. A (84 larvae), and *Nansenia* sp. B. (2 larvae). The specific identities of the two kinds of *Nansenia* larvae are still uncertain. On EASTROPAC I, *Nansenia* sp. A was taken most commonly in an equatorial band between lat 5° N and 5° S (Fig. 2). Larvae of *Nansenia* sp. A also occur in the southern portion of the area surveyed on cruises of CalCOFI, particularly to the south of Point San Eugenio, Baja California. A *Nansenia* larva with markedly different pigmentation pattern was obtained at station 11.154 in the central water mass of the South Pacific. A similarly pigmented *Nansenia* larva was obtained on NORPAC from the central water mass of the North Pacific.

4. BATHYLAGIDAE
(304 occurrences, 4,880 larvae)

Although two kinds of *Bathylagus* larvae were obtained, one species was taken in only two contiguous southern stations, 12.142 and 12.144. The eyes of the latter were carried on short stalks. The distribution of larvae of the commonly occurring species, *B. nigrigenys* Parr (296 occurrences, 2,987 larvae), was almost identical with that of the myctophid, *Diogenichthys laternatus* (Garman) (Fig. 3). The larvae of neither species occurred in the central South Pacific water mass; on the four outer lines, surveyed by *Argo* and *Jordan*, the occurrences of *B. nigrigenys* larvae ended at about lat 5° S. In the portion of the EASTROPAC area in which larvae of this species were distributed, they occurred in three-fourths of the stations occupied.

In the innermost pattern occupied by *Alaminos*, larvae of *Leuroglossus stilbius urotranus* (Bussing, 1965) were common (37 occurrences, 1,890 larvae). All but four specimens were obtained between lat 10° N and 10° S, and most within 300 miles of the coast (Fig. 2).

5. GONOSTOMATIDAE
(459 occurrences, 22,046 larvae)

Areal occurrence and relative abundance of gonostomatid larvae on EASTROPAC I are summarized in Table 9. They were obtained in 95 % of the hauls and made up approximately 23.2 % of the larvae.

As noted earlier, gonostomatid larvae were markedly more abundant in night hauls than in day hauls: 4.35 times as many, on the average. In contrast, larvae of the closely related hatchetfishes, Sternoptychidae, were taken in only slightly larger numbers at night (1.24 times as many as in day hauls). In the section dealing with depth distribution of fish larvae it was pointed out that the gonostomatid, *Vinciguerria* spp. occurred no deeper than ca. 130 m in NORPAC collections, whereas sternoptychid larvae were inhabitants of the aphotic zone below 130 m. An interesting exception should be noted: gonostomatid larvae of the subfamily Maurolicinae had depth distributions similar to sternoptychid larvae on NORPAC. Larvae of two Maurolicinae, *Maurolicus* and *Araiophos*, genera were taken on EASTROPAC. Although the depth distribution of these genera has not

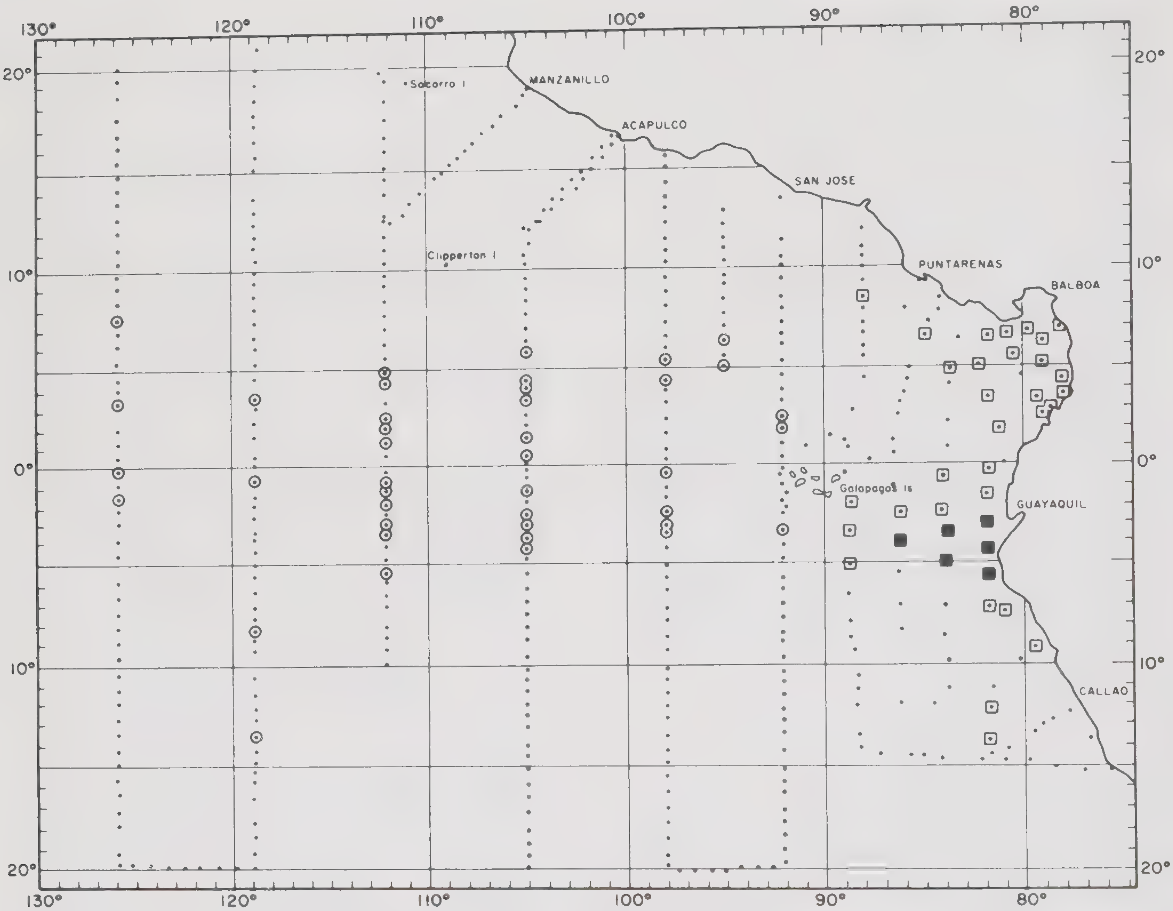
130°
120°
110°
100°
90°
80°
20°
10°
0°
10°
20°
Socorro I
MANZANILLO
ACAPULCO
SAN JOSE
Clipperton I
PUNTARENAS
BALBOA
Galapagos Is
GUAYAQUIL
CALLAO

FIGURE 2.—Distribution of larvae of the argentinid, *Nansenia* spp., and of the bathylagid, *Leuroglossus stilbius urotranus* (Bussing) on EASTROPAC I. Records of occurrence of *Nansenia* larvae are shown as open circles with dot in center, while those of *Leuroglossus* larvae are open squares with dot (1 to 100 larvae) or closed squares (101 to 490 larvae). Small solid circles represent other stations occupied on EASTROPAC I.

TABLE 9.—Areal occurrence and relative abundance of larvae of Gonostomatidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-15° N	16	418	20	1,534	5	115	--	--	41	2,067	50.4
15° N-10° N	14	380	22	745	24	607	--	--	60	1,732	28.9
10° N- 5° N	13	185	13	242	27	2,085	14	417	67	2,929	43.7
5° N- 0°	14	2,112	15	637	14	1,825	27	1,882	70	6,456	92.2
0° - 5° S	14	409	18	912	14	1,577	16	1,036	62	3,934	63.5
5° S-10° S	13	202	14	161	14	799	10	647	51	1,809	35.5
10° S-15° S	14	635	8	368	15	524	21	490	58	2,017	34.8
15° S-20° S	20	322	8	183	22	597	--	--	50	1,102	22.0
Total	118	4,663	118	4,782	135	8,129	88	4,472	459	22,046	48.0

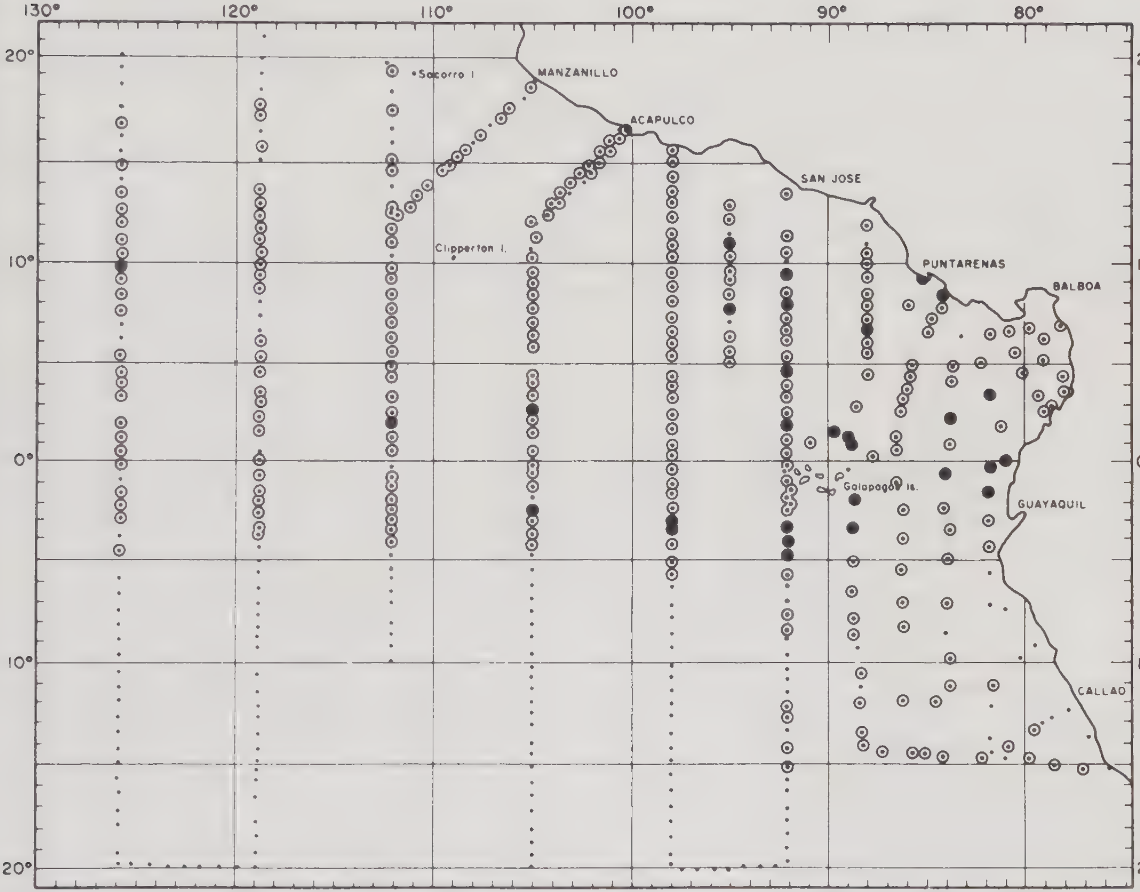

FIGURE 3.—Distribution of larvae of *Bathylagus nigrigenys* Parr on EASTROPAC I. Two orders of abundance are shown: open circles with dot in center represent counts of 1 to 25 larvae, large solid circles represent counts of 26 or more larvae. Small solid circles represent negative hauls.

been determined, they were sampled more fully during daylight hours than other gonostomatids; the night/day ratio for *Maurolicus* and *Araiophos* larvae was ca. 1.6 and 2.0 respectively.

Larvae belonging to six gonostomatid genera were common to abundant (Table 10) and larvae of several additional genera were taken occasionally. Larvae of two genera were of outstanding importance in the EASTROPAC area—*Vinciguerria* and *Cyclothone*. *Vinciguerria occurred* in 87.5 % of the collections, *Cyclothone* in 62.4 %.

Charts showing the distribution and relative abundance of larvae of Gonostomatidae and Sternoptychidae (combined) on EASTROPAC I will be included in the EASTROPAC Atlas.

Araiophos eastropas Ahlstrom and Moser (18 occurrences, 529 larvae)

Larvae of *Araiophos eastropas* were obtained only on the outermost pattern to the south of lat 10° S (Fig. 4). Within this limited area it was the most common gonostomatid. The species taken on EASTROPAC represented an undescribed species in a genus that previously

TABLE 10.—Frequency of occurrence and relative abundance of the kinds of gonostomatid larvae on EASTROPAC I.

Gonostomatid larvae	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
Araiophos eastropas	18	529	0	0	0	0	0	0	18	529
Cyclothone spp.	94	697	71	582	89	735	47	167	301	2,181
Diplophos taenia	18	51	40	107	14	24	1	1	73	183
Ichthyococcus spp.	7	9	11	16	18	31	5	5	41	61
Maurolicus muelleri	0	0	11	43	19	143	13	78	43	264
Vinciguerria spp.	96	3,339	109	4,011	131	7,179	86	4,211	422	18,740
Other gonostomatids	13	38	9	23	12	17	8	10	42	88
Total	118	4,663	118	4,782	135	8,129	88	4,472	459	22,046

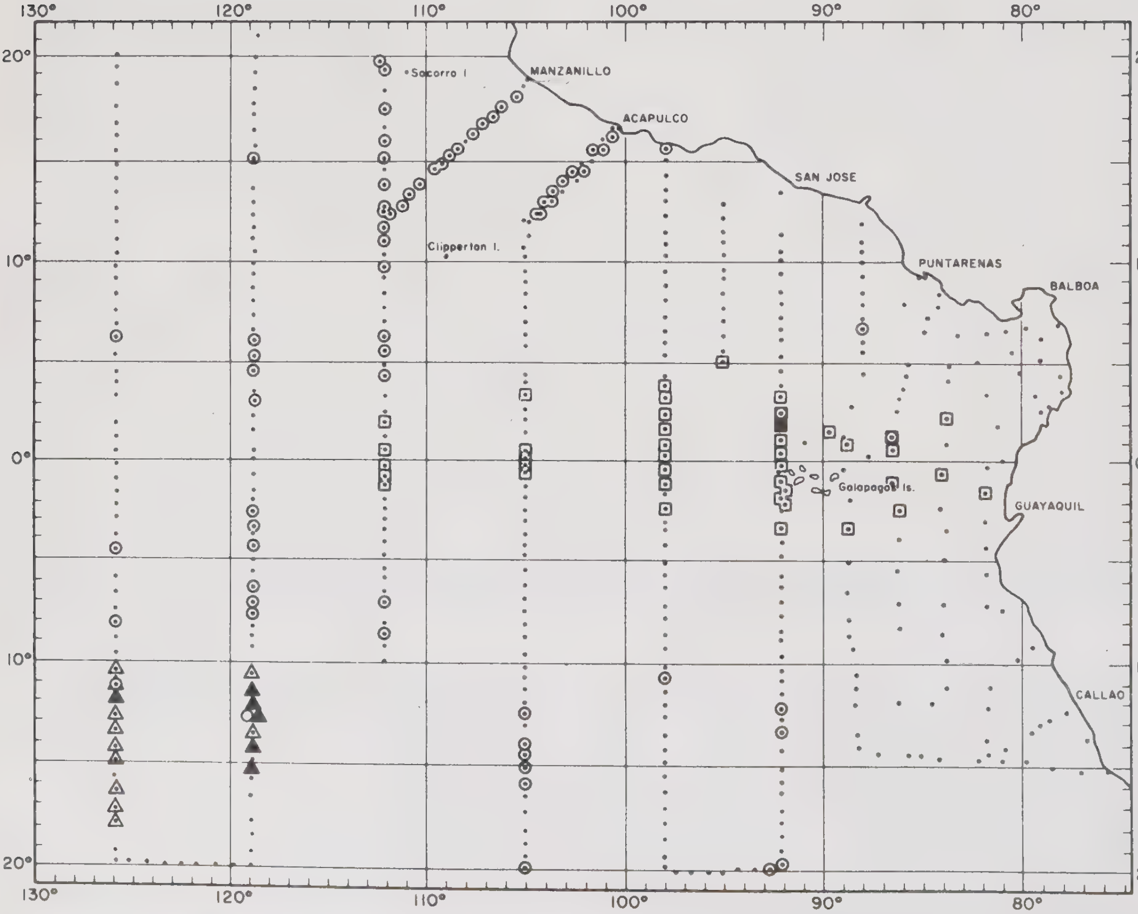
130°
120°
110°
100°
90°
80°
20°
10°
0°
10°
20°
Socorro I
MANZANILLO
ACAPULCO
SAN JOSE
Clipperton I.
PUNTARENAS
BALBOA
Galapagos Is.
GUAYAQUIL
CALLAO

FIGURE 4.—Distribution of larvae of three species of Gonostomatidae on EASTROPAC I. Records of occurrence of larvae of *Araiophos eastropas* Ahlstrom and Moser are shown as triangles, *Diplophos taenia* (Günther) as large open circles, and *Maurolicus muelleri* (Gmelin) as squares. Solid triangles and squares are for counts of 26 or more larvae. Small solid circles represent negative hauls.

was known from a single collection made off Hawaii (Grey, 1961). Adults and larvae were described by Ahlstrom and Moser (1969).

Cyclothone spp. (301 occurrences, 2,181 larvae)

Larvae of *Cyclothone* spp. were taken least frequently in the northern quarter of the EASTROPAC pattern (betweeen lat 10° and 20° N, and in the inner pattern occupied by *Alaminos* (Table 11 and Fig. 5). In the former area, less than 20 % of the hauls (20 of 103) contained *Cyclothone* larvae; in the inshore pattern only about 45 % of the hauls (47 of 103) contained *Cyclothone* larvae. Over the remainder of the EASTROPAC I pattern *Cyclothone* larvae occurred at most stations (234 of 276). The lowest number of larvae per positive haul, 2.15 larvae, was obtained in the northern section; the next lowest, 3.55 larvae per positive haul, in the *Alaminos* pattern. Over the remainder of the pattern, 8.42 larvae were obtained per positive haul.

No attempt was made to identify the larvae of *Cyclothone* to species, and our hauls did not extend deep enough to collect adults.

Diplophos taenia Günther (73 occurrences, 183 larvae)

A study was made of larval and adult specimens of *Diplophos* in an attempt to determine whether the Pacific specimens should be assigned to *D. taenia* or retained as a distinct species, *D. pacificus* Günther. Grey (1960) had placed Pacific specimens in *D. taenia* but later she (Grey, 1964, p. 89) developed reservations because of the consistently lower photophore count of the ventral series in Pacific specimens. Without detailing my observations on *Diplophos*, which I plan to publish separately, I have concluded that our eastern Pacific *Diplophos* is not separable from the Atlantic *D. taenia*.

Larvae of *Diplophos* were taken most commonly to the north of lat 10° N—36 occurrences, 105 larvae (Fig. 4). The remaining 37 occurrences, 78 larvae were distributed throughout the EASTROPAC I pattern.

Ichthyococcus spp. (41 occurrences, 61 larvae)

Two kinds of *Ichthyococcus* larvae were taken on EASTROPAC I. The specific identity of the more common form has been determined as *I. irregularis* Rechnitzer and Böhlke; the other form has yet to be identified to species.

Maurolicus muelleri (Gmelin) (43 occurrences, 264 larvae)

Larvae of this species were taken only on an equatorial band between lat 5° N and 5° S and were not taken in the outer pattern occupied by *Argo* (Fig. 4). This distribution, without additional information, could be misleading. *Maurolicus* is known to have a wide latitudinal distribution in the South Pacific. For example, *Maurolicus* larvae were obtained at lat 33° S on MARCHILE VI, the portion of EASTROPAC II occupied by the Chilean vessel *Yelcho*. We also have collections from south of New Zealand, obtained on an *Eltanin* cruise. The species may be carried northward off South America in the Humboldt Current and then offshore in the equatorial current system.

TABLE 11.—Areal occurrence and relative abundance of larvae of *Cyclothone* spp. on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-10° N	12	31	4	8	4	4	--	--	20	43	2.2
10° N- 0°	24	136	25	137	33	235	23	69	105	577	5.5
0° -10° S	24	179	29	246	20	117	13	43	86	585	6.8
10° S-20° S	34	351	13	191	32	379	11	55	90	976	10.8
Total	94	697	71	582	89	735	47	167	301	2,181	7.2

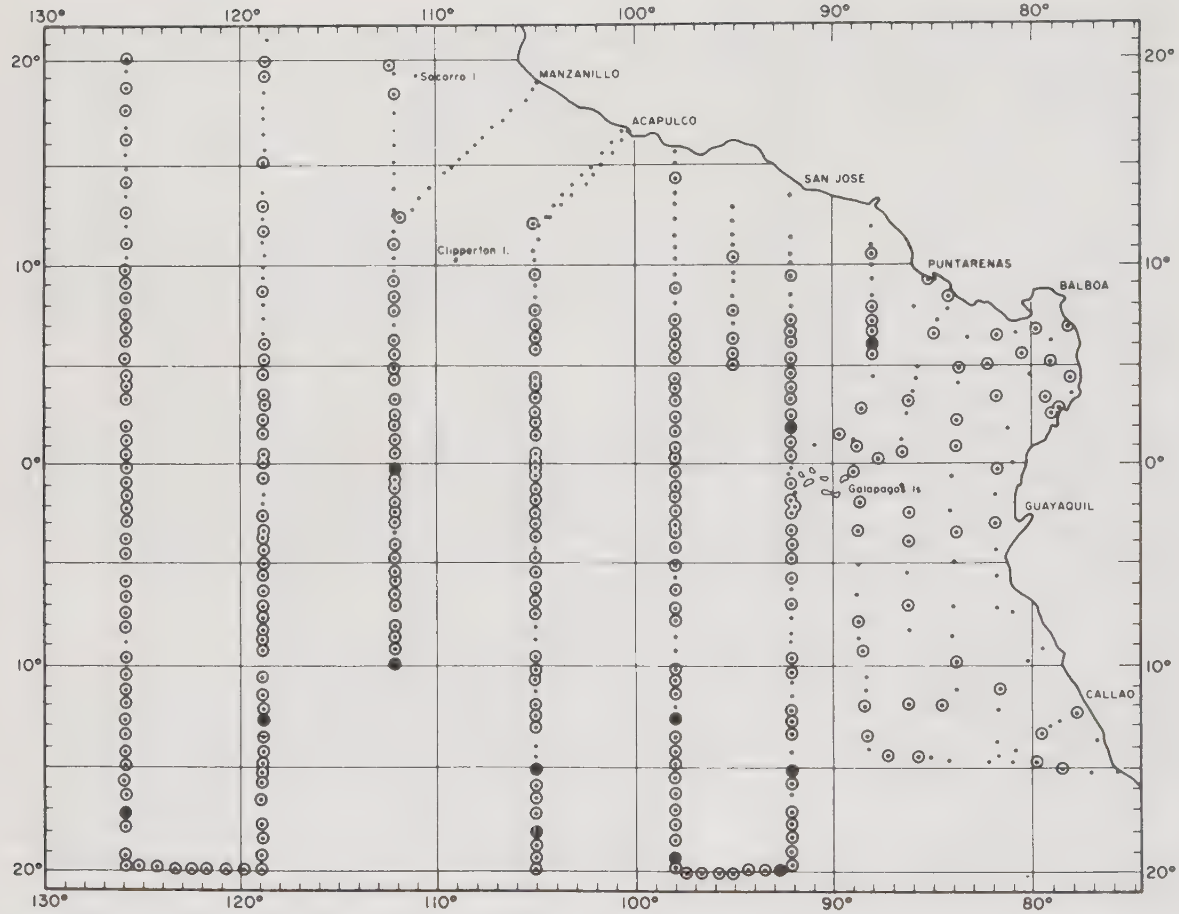

FIGURE 5.—Distribution of larvae of the gonostomatid *Cyclothone* spp. on EASTROPAC I. Collections of 1 to 25 larvae are shown as circles with dot in center, collections of 26 or more larvae as large solid circles; negative hauls are shown as small solid circles.

Vinciguerria spp. (422 occurrences, 18,740 larvae)

Larvae of *Vinciguerria* occurred in more hauls than those of any other genus and ranked second in abundance to the myctophid genus *Diogenichthys*. The distribution of *Vinciguerria* larvae is shown in Figure 6. Although most of the material unquestionably is *V. lucetia* (Garman), some of the collections from offshore and particularly from the central South Pacific water mass between lat 5° and 20° S represent *V. nimbaria* (Jordan and Williams). The larvae of *V. nimbaria* are indistinguishable from those of *V. lucetia* (Ahlstrom and Counts, 1958), hence identification must be made on metamorphosing specimens, juveniles, and adults. The two species are closely allied, but readily separable from *V. poweriae* (Cocco) and *V. attenuata* (Cocco), the other two species of *Vinciguerria*, at all stages of development. A trenchant difference between the two "pairs" of species is the development of a pair of symphyseal photophores under the lower jaw in *V. lucetia* and *V. nimbaria* and the absence of this pair in *V. poweriae* and *V. attenuata*. The two characters most readily used for distinguishing

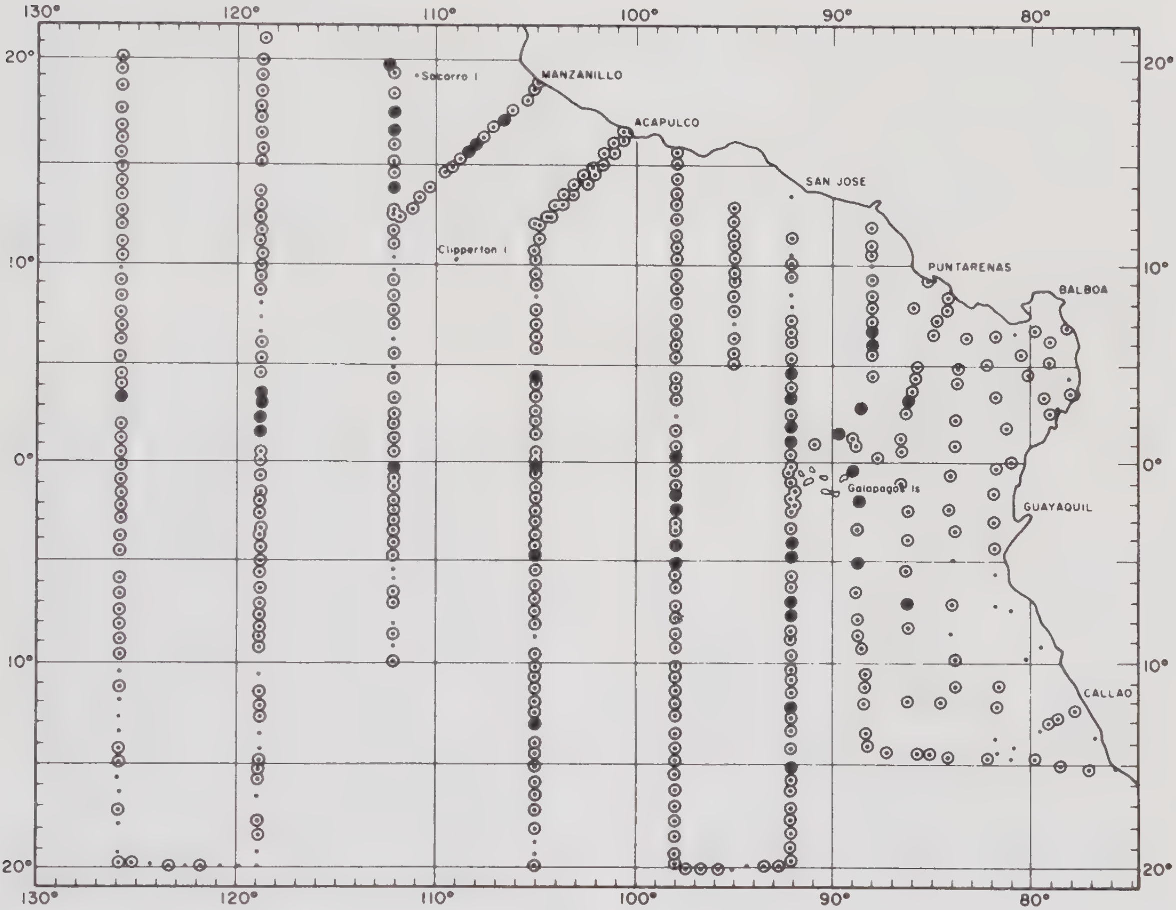

FIGURE 6.—Distribution of larvae of the gonostomatid, *Vinciguerria* spp. on EASTROPAC I. Collections of 1 to 100 larvae are shown as circles with dot in center, collections of 101 or more larvae as large solid circles; negative hauls are shown as small solid circles.

between *V. lucetia* and *V. nimbaria* are (1) number of gill rakers and (2) number of IV (and OV) photophores. Material of *V. nimbaria* studied from the eastern North Pacific (ibid.) had 5 to 6 + 15 gill rakers and 23 to 24 IV photophores (13 to 14 OV photophores) whereas *V. lucetia* had 8 to 10 + 18 to 23 gill rakers and 20 to 23 IV photophores (10 to 13 OV photophores). In the EASTROPAC area, *V. lucetia* maintained the high gill raker counts, but usually had 21 IV (11 OV) photophores. The offshore form referred to *V. nimbaria* usually had 22 IV (12 OV) photophores (1 less per group than in *V. nimbaria* from the temperate North Pacific) and 6 to 7 + 15 to 16 gill rakers (a slightly higher count).

In most areas the adults of the two species of *Vinciguerria* did not co-occur, hence the larvae can be assigned with some assurance to one or the other. For example, all collections made between lat 5° and 20° S from *Argo* and *Jordan* patterns were exclusively *V. nimbaria*. On these patterns the plankton hauls were supplemented by micronekton net hauls, and the latter contained material of *Vinciguerria* juveniles and adults from most stations occupied at night. Unfortunately, the micronekton net was not used on *Rockaway* (12.000 series), and insufficient numbers of older stages (metamorphosing specimens and juveniles) were taken in plankton hauls to permit a meaningful separation of the two species in waters to the south of lat 5° S in this series.

Vinciguerria poweriae (Cocco) co-occurred with *V. nimbaria* in the central water mass of the North Pacific (Ahlstrom and Counts, 1958), but no material of *V. poweriae* was obtained in EASTROPAC collections. However, material of *V. attenuata* (Cocco) was obtained from farther south in the eastern Pacific on the "Downwind Expedition"—hence all four species of *Vinciguerria* do occur in the eastern Pacific.

Other gonostomatids (42 occurrences, 88 larvae)

Included in this category are larvae of two identified genera, *Gonostoma* and *Woodsia*, and several kinds of larvae that are unmistakably gonostomatid, but not identified as to kind.

6. STERNOPTYCHIDAE

(337 occurrences, 5,687 larvae)

Hatchetfish larvae ranked third in abundance (5.98 % of total), exceeded by larvae of Myctophidae and Gonostomatidae. The majority of hatchetfish larvae were those of *Sternoptyx diaphana* Hermann, and most of the remainder of *Argyropelecus lychnus* Garman. Because larvae of Sternoptychidae are more fragile than most other kinds and are usually in poor condition, no attempt was made to identify them to genus or species. Areal occurrence and relative abundance of sternoptychid larvae on EASTROPAC I are summarized in Table 12. Larvae were not only taken in markedly more collections between lat 10° N and 10° S—94 % of the collections were positive as compared with only 41 % in the remainder of the pattern—but more larvae were taken per positive haul—21.1 larvae as compared with 5.2.

7. ASTRONESTHIDAE

(12 occurrences, 13 larvae)

Several kinds of astronesthid larvae were collected in the EASTROPAC area: only one kind had heavy pigmentation on the body; the others were lightly, but characteristically pigmented. Larvae of Astronesthidae are similar in appearance to other stomiatoid larvae; they have a slender, elongated body, and a long intestine that underlies the body for about $\frac{7}{10}$ or more of the standard length, and usually has a free terminal, trailing portion that can be quite long, often trailing beyond the caudal fin. Astronesthid larvae can be distinguished readily from other stomiatoid larvae by the forward position of the dorsal fin in relation to the anal fin. Developmental series of astronesthid larvae have not been described in literature. Eleven of the 12 occurrences of astronesthid larvae were taken within 10° ± of the equator.

8. CHAULIODONTIDAE

(80 occurrences, 165 larvae)

Larvae of *Chauliodus* are readily identifiable to genus, but are difficult to separate at the spe-

TABLE 12.—Areal occurrence and relative abundance of larvae of Sternoptychidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-15° N	8	44	0	0	0	0	--	--	8	44	5.5
15° N-10° N	6	41	3	31	9	66	--	--	18	138	7.7
10° N- 5° N	14	312	14	479	29	1,006	14	237	71	2,034	28.6
5° N- 0°	14	133	15	430	13	456	22	414	64	1,433	22.4
0° - 5° S	14	140	18	353	14	303	16	129	62	925	14.9
5° S-10° S	12	198	14	317	14	210	10	104	50	829	16.6
10° S-15° S	13	40	8	98	11	83	5	7	37	228	6.2
15° S-20° S	9	15	2	4	16	37	--	--	27	56	2.1
Total	90	923	74	1,712	106	2,161	67	891	337	5,687	16.9

cies level, because of lack of pigmentation. It has not been determined yet whether one or more species of *Chauliodus* occur in the EASTROPAC area. *Chauliodus* larvae were widely distributed, usually occurring singly (50 such occurrences). In only five hauls were six or more larvae obtained per haul; all of these were in the outer patterns occupied by *Jordan* and *Argo*.

9. IDIACANTHIDAE
(167 occurrences, 960 larvae)

It is not known definitely whether one or two species of *Idiacanthus* occur in the eastern Pacific; the problem hinges on whether *I. panamensis* is distinct from *I. antrostomus* Gilbert. Gibbs (1964) considered the two species to be "probably synonymous." In the EASTROPAC area, *Idiacanthus* occurred more frequently in the northern portion of the pattern, between lat 10° and 20° N, as is shown in Table 13.

10. OTHER STOMIATOIDEI
(203 occurrences, 502 larvae)

Larvae belonging to three families are included as other Stomiatoidei—i.e., of Stomiatidae, Melanostomiatidae, and Malacosteidae. The most common larva in this category, that of *Bathophilus filifer* (Garman) (86 occurrences, 227 larvae) is separately tabulated in Appendix Table 3. Larvae of *Eustomias*, representing several species, occurred in 17 collections. Larvae of *Stomias* were separately tabulated from only eight collections; however, a number of larvae tabulated as unidentified stomiatoid larvae undoubtedly are those of *Stomias*. According to Gibbs (1969), no fewer than three species of *Stomias* occur in the eastern Pacific. Many stomiatoid larvae were poorly preserved, and were not identifiable with any certainty.

11. SYNODONTIDAE
(10 occurrences, 41 larvae)

All but three specimens were taken in the inner pattern, occupied by *Alaminos*. Six of the seven occurrences in this pattern were at contiguous stations occupied off Ecuador and the Gulf of Panama (Fig. 7). Synodontidae are coastal forms. No attempt was made to identify the larvae to the species level.

12. CHLOROPHTHALMIDAE
(1 occurrence, 4 larvae)

The only record of *Chlorophthalmus* larvae was from station 13.052. Larvae in this sample ranged from 5.0 to 6.5 mm long. Pigmentation was limited to a large, single peritoneal pigment patch—and to a few small melanophores on the dorsal and ventral margin of the tail soon before the tip of the notochord. Two larger specimens of *Chlorophthalmus* were taken in the micronekton net hauls, a 23.0-mm specimen at station 14.018 and a 39.5-mm specimen at station 14.051. Pigment on both was limited to the peritoneal patch, and a midline melanophore over the hypural complex; otherwise both specimens were milky white, without scales. The larger specimen had the following fin counts: D. 11, A. 11, V. 9, P. 17. These are identical to counts given by Garman (1899) for his species, *C. mento* from the Gulf of Panama, to which our material probably is referable.

TABLE 13.—Areal occurrence and relative abundance of larvae of Idiacanthidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-10° N	18	107	34	379	17	149	--	--	69	635	9.2
10° N- 0°	11	19	7	10	14	65	20	56	52	150	2.9
0° -10° S	4	6	2	4	7	44	4	9	17	61	3,6
10° S-20° S	9	15	3	4	8	53	9	42	29	114	3.9
Total	42	147	46	395	46	311	33	107	167	960	5.7

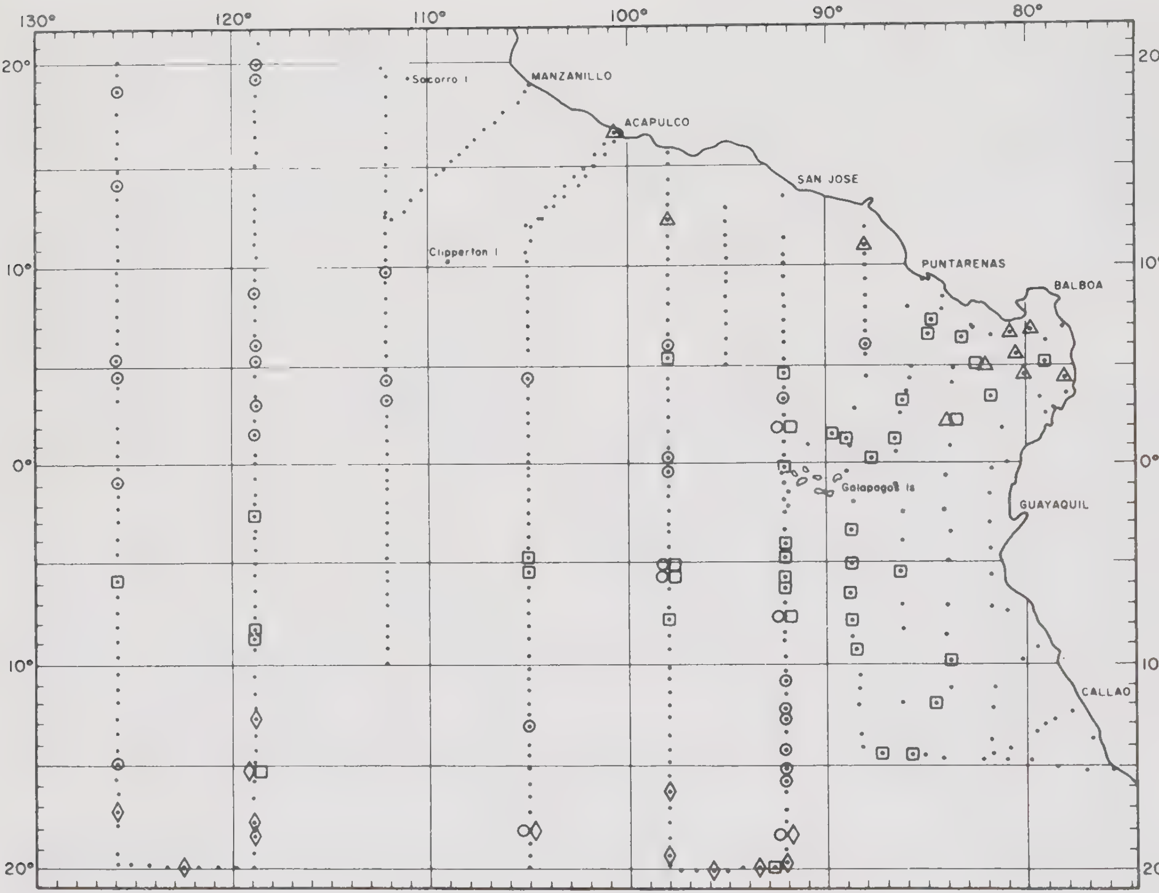

FIGURE 7.—Distribution of larvae of the paralepidids, *Macroparalepis macrurus* Ege and *Sudis atrox* Rofen, of *Synodus* spp., and of the gempylid *Nealotus tripes* Johnson on EASTROPAC I. Records of occurrence of larvae of *Macroparalepis macrurus* are shown as an open circle, larvae of *Sudis atrox* as a diamond, larvae of *Synodus* spp. as a triangle, and larvae of *Nealotus tripes* as a square; negative hauls are shown as small solid circles.

13. MYCTOPHIDAE

(472 occurrences, 44,913 larvae)

Myctophids made up 47.2% of the fish larvae taken on EASTROPAC I. Of the 482 oblique hauls taken on EASTROPAC I, 472 contained myctophid larvae. This dominant group occurred almost everywhere. However, as is shown in Table 14, larger numbers of myctophid larvae were taken per haul between lat 10° N and 5° S.

The myctophid fauna is a large one in numbers of genera and species represented in the eastern tropical Pacific. This diversity is shown in Table 15, in which occurrence and abundance of myctophid larvae are summarized by genus or species; the number of genera listed is 19. Even so, larvae of *Diogenichthys laternatus* made up over half of the total.

The study of larval myctophids is aided by the diversity of larval morphology found in this family, and by the fact that the larvae of most genera have a characteristic form that permits identification to genus, even for genera in which the species composition has not been fully worked out. This point was stressed in two recent papers dealing with identification of myctophid larvae (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1970).

Because of the importance of this group in the tropical ichthyoplankton, I will discuss its composition in more detail than for any other family except the Gonostomatidae.

Moser and Ahlstrom (1970) described developmental series for 14 species of lanternfishes with narrow-eyed larvae in the California Current. The following species also occur in the EASTROPAC area: *Electrona rissoi, Diogenichthys atlanticus, D. laternatus, Benthosema panamense, Hygophum atratum, H. reinhardti, Myctophum nitidulum, Loweina rara, Gonichthys tenuiculus,* and *Centrobranchus choerocephalus.*

TABLE 14.—Areal occurrence and relative abundance of larvae of Myctophidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-15° N	16	430	20	1,000	5	116	--	--	41	1,546	37.7
15° N-10° N	14	568	23	1,444	24	2,826	--	--	61	4,838	79.3
10° N- 5° N	14	1,323	14	2,136	29	5,856	15	2,730	72	12,045	167.3
5° N- 0°	14	1,988	15	2,327	14	1,325	27	6,075	70	11,715	167.4
0° - 5° S	14	1,233	18	3,413	14	1,635	16	1,209	62	7,490	120.8
5° S-10° S	13	567	15	408	14	994	13	635	55	2,604	47.3
10° S-15° S	14	563	8	296	15	1,362	25	768	62	2,989	48.2
15° S-20° S	19	321	8	250	22	1,115	--	--	49	1,686	34.4
Total	118	6,993	121	11,274	137	15,229	96	11,417	472	44,913	95.2

TABLE 15.—Summary, by genus or species, of occurrences and relative abundance of myctophid larvae in the four vessel patterns occupied on EASTROPAC I.[1]

Myctophid larvae	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
Benthosema panamense	0	0	1	63	5	918	1	46	7	1,027
Centrobranchus spp.	0	0	3	4	0	0	0	0	3	[2]4
Ceratoscopelus townsendi-complex	46	235	24	140	42	633	5	12	117	1,020
Diaphus spp.	62	490	96	1,363	72	949	21	71	251	2,873
Diogenichthys laternatus	69	2,202	89	5,259	92	9,089	89	8,775	339	25,325
Diogenichthys atlanticus	3	4	6	11	18	75	2	2	29	92
Electrona sp.	5	6	9	34	19	34	0	0	33	74
Gonichthys tenuiculus	5	8	20	56	39	101	28	67	92	232
Gonichthys sp.	0	0	0	0	0	3	0	0	3	3
Hygophum atratum & *H. reinhardti*	30	177	52	352	37	268	8	90	127	887
Hygophum proximum	67	611	30	215	19	72	0	0	116	898
Lampadena spp.	13	27	10	21	15	71	0	0	38	119
Lampanyctus spp.	99	1,240	96	2,063	107	1,347	74	1,232	376	5,882
Lepidophanes pyrsobolus-complex	7	26	14	109	10	22	3	6	34	163
Lobianchia sp.	2	14	2	3	12	22	0	0	16	39
Loweina rara	18	25	7	11	13	14	4	5	43	56
Myctophum spp.	52	624	48	323	47	160	40	286	187	1,393
Notolynchus valdiviae	40	210	47	290	60	344	11	24	158	868
Notoscopelus resplendens	13	37	21	104	21	73	15	69	70	283
Protomyctophum sp.	3	4	19	37	14	37	0	0	36	78
Symbolophorus evermanni	71	535	47	248	58	381	36	318	212	1,482
Triphoturus spp.	17	33	25	82	54	256	44	135	140	506
Unidentified myctophid larvae	39	98	36	65	62	190	26	56	163	409
Disintegrated myctophid larvae	75	387	60	423	64	170	42	223	241	1,203
Total myctophid larvae	118	6,993	121	11,274	137	15,229	96	11,417	472	44,913

[1] The table summarizes the data presented by individual station in Appendix Table 2.

[2] *Centrobranchus* larvae are included under unidentified myctophid larvae in Appendix Table 2.

Benthosema panamense (Tåning) (7 occurrences, 1,027 larvae)

The relatively large number of larvae taken in a few hauls probably results from the adults of this species occurring in more compact aggregations than other myctophids (Alverson, 1961). All occurrences were within a few hundred miles of the coast, mostly off Mexico and Costa Rica. Distribution of larvae of *B. panamense* in the eastern tropical Pacific was illustrated in Moser and Ahlstrom (1970).

Centrobranchus spp. (3 occurrences, 4 larvae)

The larvae assigned to *Centrobranchus* represent two kinds; one of these is identical to the larvae described as *C. choerocephalus* (Moser and Ahlstrom, 1970). The other is possibly *C. andrae.*

Ceratoscopelus townsendi-complex (117 occurrences, 1,020 larvae)

Until recently, only two species of *Ceratoscopelus* were recognized: *C. townsendi* (Eigenmann and Eigenmann) and *C. maderensis* (Lowe). The larvae of these two species are distinctively different, especially in pigmentation. Nafpaktitis and Nafpaktitis (1969) concluded that *C. warmingi* (Lutken) was distinct from *C. townsendi* and was the more widely distributed species. They indicated that *C. townsendi* probably was restricted in its distribution to the eastern North Pacific. The major difference between the two species is the presence on *C. townsendi* of a large patch of luminous tissue along the dorsal rim of the orbit on specimens larger than ca. 21 mm SL; otherwise, the two species are almost identical in meristic characters, arrangement of photophores, and the placement of most luminous patches.

Subsequent to the publication of the paper by Nafpaktitis and Nafpaktitis (1969), my colleague, H. G. Moser, and I studied developmental series of *Ceratoscopelus* larvae previously assigned to *C. townsendi.* Moser (unpublished) studied eastern North Pacific material (CalCOFI and NORPAC) and material from the eastern South Pacific obtained on EASTROPAC I; I had the opportunity to examine a number of collections of *Ceratoscopelus* larvae collected by the *Meteor* in the Indian Ocean (through the generosity of W. Nellen of the Institut für Meereskunde, University of Kiel, Germany). Based on criteria of Nafpaktitis and Nafpaktitis, adults from both the Indian Ocean and southern portion of the EASTROPAC area were referable to *C. warmingi,* those from CalCOFI and NORPAC to *C. townsendi.* Larvae from the three regions were strikingly similar in appearance. Observed differences were mostly in rate of development, particularly in the sizes at which fin formation took place and at which photophores developed. Even so, somewhat greater differences were observed between *Ceratoscopelus* larvae from the Indian Ocean and those from the EASTROPAC area, than between larvae from the two eastern Pacific regions. For the present, I choose to call attention to the complexity of this problem by referring EASTROPAC material to the *C. townsendi*-complex.

Distribution of *C. townsendi*-complex larvae on EASTROPAC I is illustrated in Figure 8. Most occurrences were in offshore waters between lat 5° and 20° S, i.e., in the South Pacific central water mass. *Ceratoscopelus* larvae are known to have a complementary distribution in the eastern North Pacific. On the NORPAC Expedition *Ceratoscopelus* larvae were the dominant myctophid in the North Pacific central water mass between ca. lat 20° and 40° N. The occurrences of *Ceratoscopelus* larvae in the *Argo* pattern between lat 17° and 20° N are a fragment of this northern population. The few occurrences of *Ceratoscopelus* larvae in waters of the equatorial current system were small individuals. A few adults also were collected in this region, hence tropical waters may not be a barrier to the interchange of fish between the populations in the North and South Pacific.

Diaphus spp. (251 occurrences, 2,873 larvae)

Diaphus, the genus of myctophids with the largest number of species, is represented in the tropical eastern Pacific by a number of larval forms whose specific identities have been worked out only partially.

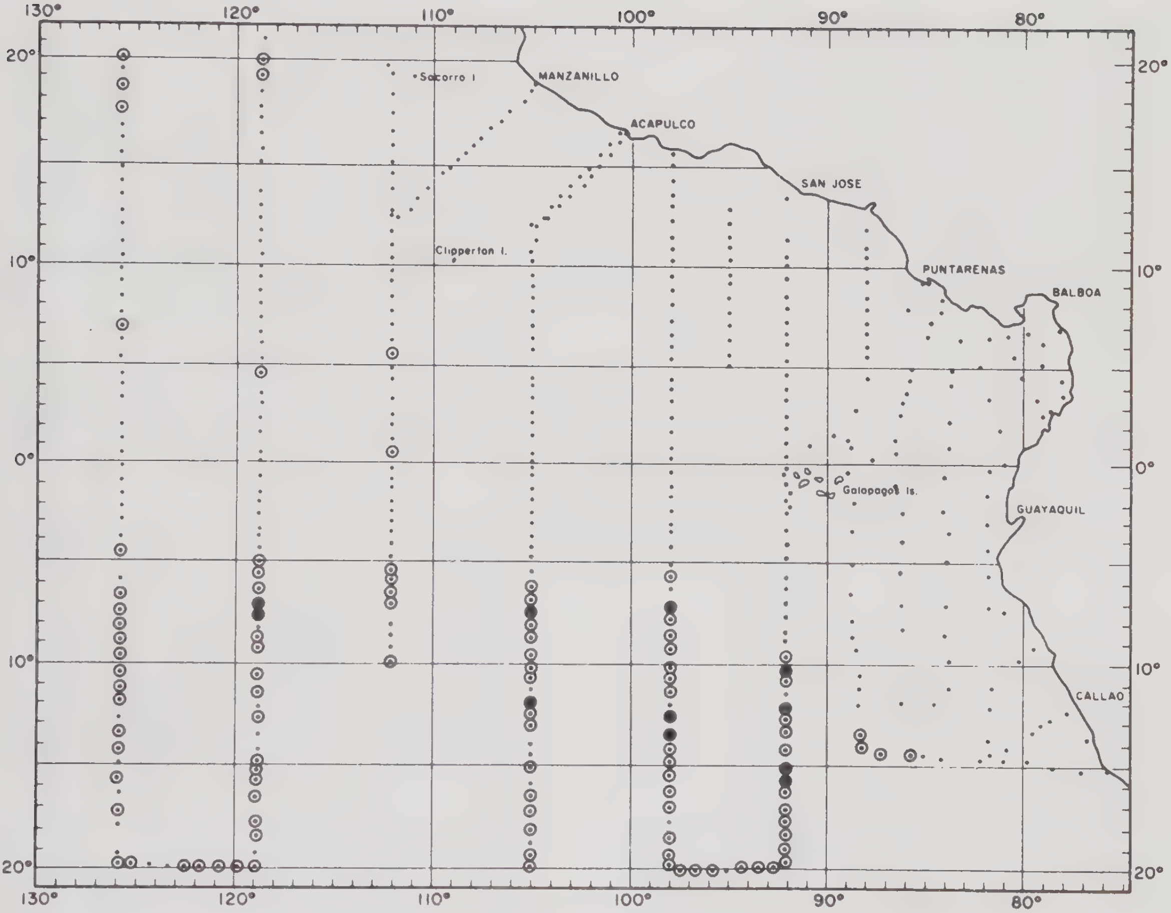

FIGURE 8.—Distribution of larvae of the myctophid, *Ceratoscopelus townsendi*-complex on EASTROPAC I. Collections of 1 to 25 larvae are shown as circles with dot in center, collections of 26 or more larvae as large solid circles; negative hauls are shown as small solid circles.

The genus *Diaphus* is not a natural assemblage, inasmuch as there are two distinctive larval morphs for the species in the EASTROPAC area. One group has slender-bodied larvae with persistent ventral midline pigment on the tail; the adults of this group possess both Vn and So occular photophores (subgenus *Diaphus* of Fraser-Brunner, 1949). The other and larger group has stubby-bodied larvae which usually are but lightly pigmented; in the EASTROPAC area the larvae of *Diaphus pacificus* Parr is a representative example.

Although *Diaphus* larvae were distributed over most of the area covered on EASTROPAC I, they were least common in the inner pattern occupied by *Alaminos* (21 occurrences, 71 larvae) and most consistently taken in the intermediate pattern occupied by *Jordan* (96 occurrences, 1,363 larvae).

Diogenichthys laternatus (Garman) (339 occurrences, 25,325 larvae)

Although this is by far the most abundant kind of larva taken on EASTROPAC I, it did not occur in the central water mass of the South

Pacific (Fig. 9). This species similarly is absent from the central water mass of the North Pacific (Moser and Ahlstrom, 1970). There is a striking similarity in the distributions of larvae of *D. laternatus* and those of *Bathylagus nigrigenys* Parr (Fig. 3) in the EASTROPAC area. *D. laternatus* is one of the smaller species of myctophids, measuring only 20.0 to 30.0 mm as adults; hence its biomass probably is not as great as its larval abundance would suggest.

Diogenichthys atlanticus **(Tåning)**
(29 occurrences, 92 larvae)

In contrast to its cogener, larvae of *Diogenichthys atlanticus* were taken mostly in the central water mass of the South Pacific on EASTROPAC I (Fig. 9). Most of the occurrences were to the south of lat 10° S on three adjacent lines (along long 92°, 98°, and 115° W). Two occurrences at the southern end of the *Alaminos* pattern, however, indicate that this

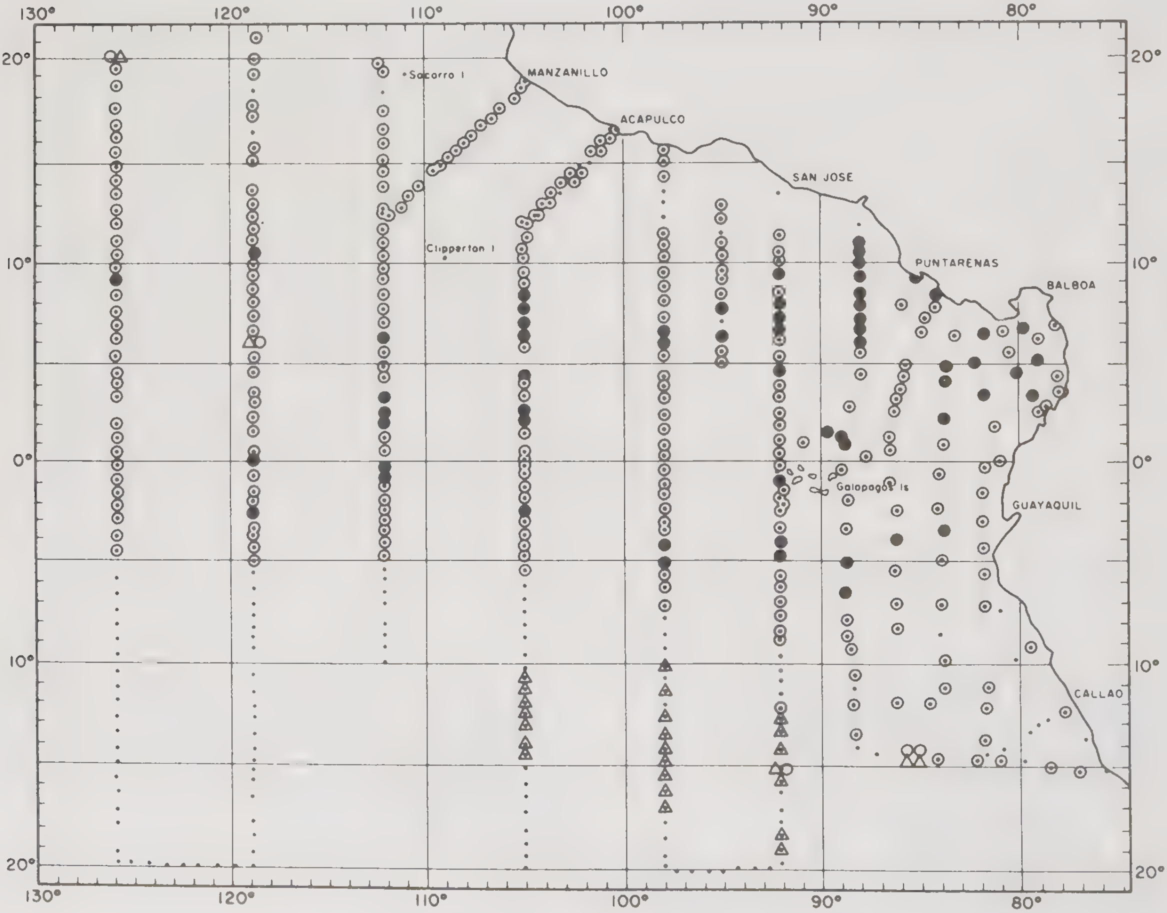

FIGURE 9.—Distribution of larvae of two species of myctophids of the genus *Diogenichthys* on EASTROPAC I. Records of occurrence of larvae of *D. atlanticus* (Tåning) are shown as triangles, records of occurrences of larvae of *D. laternatus* (Garman) as large circles with dot in center for hauls containing 0 to 100 larvae, and as large solid circles for hauls containing 101 or more specimens of this species; negative hauls are shown as small solid circles.

species is not restricted to the central water mass but also can occur in the transitional waters of the Humboldt Current. Larvae of this species were taken close to the Chilean coast between lat 20° and 30° S on MARCHILE VI, the Chilean contribution to EASTROPAC II. *D. atlanticus* appears to be a temperate-subtropical species, whereas *D. laternatus* is a tropical-subtropical species. The distribution of larvae of this species in the eastern North Pacific is given in Moser and Ahlstrom (1970, figs. 41 and 42). A larval specimen taken at lat 6° N along long 119° W shows that this species can bridge the tropical gap between its areas of usual occurrence in more temperate waters of the North and South Pacific.

Electrona sp. (33 occurrences, 74 larvae)

Distribution of *Electrona* larvae on EASTROPAC I was limited to two bands—one centering on lat 5° N (6 occurrences, 16 larvae) the other in the central water mass of the South Pacific, between lat 8° and 20° S (27 occurrences, 58 larvae). The *Electrona* larvae all resemble *E. rissoi*, although two kinds may be present.

Gonichthys tenuiculus (Garman) (92 occurrences, 232 larvae)

Larvae of *Gonichthys tenuiculus* have a similar distribution in the eastern tropical Pacific to those of *Diogenichthys laternatus*. Larvae of a different species of *Gonichthys* (3 occurrences, 3 larvae) were obtained at the southern end of the *Rockaway* pattern. Beebe and Vander Pyl (1944) reported collecting more adults of *G. tenuiculus* (reported as *Myctophum coccoi* (Cocco)), than of any other myctophid on the Arcturus Expedition to the eastern Pacific in 1925. Their collections were made on adults aggregating at the surface. Based on larval evidence, *Gonichthys tenuiculus* is only moderately common.

Hygophum atratum-reinhardti (127 occurrences, 887 larvae)

Larvae of these two species are similar in appearance and difficult to distinguish at some stages of larval development. Larvae of *Hygophum atratum* (Garman) were distributed over much of the EASTROPAC pattern; however some occurrences at the southern end of the patterns of *Rockaway, Jordan,* and *Argo* were referable to *H. reinhardti* (Lutken).

Hygophum proximum Becker (116 occurrences, 898 larvae)

Hygophum proximum is a truly oceanic species, not occurring at all in the inner pattern worked by *Alaminos,* and it was most abundant in the outer pattern occupied by *Argo* (Fig. 10). It occurs in the central water masses of the North and South Pacific, but also in the equatorial current system; the largest collection of larvae (103 specimens) was obtained at the equator.

Lampadena spp. (38 occurrences, 119 specimens)

Two and possibly three kinds of *Lampadena* larvae were obtained on EASTROPAC. A developmental series definitely has been established for only one species, *Lampadena urophaos* Paxton. The relatively few occurrences of *Lampadena* larvae on EASTROPAC I were mostly in the southern portion of the three outer vessels (24 of 38 occurrences) and most of the remainder in an offshore band lying between lat 4° and 8° N (9 occurrences).

Lampanyctus spp. (376 occurrences, 5,882 larvae)

Larvae of *Lampanyctus* were taken in more collections than those of any other myctophid genus but were not identified to species. A number of species of *Lampanyctus* occur in the EASTROPAC area, of which *L. idostigma* Parr, L. *omostigma* Gilbert, *L. parvicauda* (Parr), and *L. steinbecki* Bolin are among the more common. Larval series are being worked out for these.

Lepidophanes sp. (34 occurrences, 163 larvae)

The species of *Lepidophanes* that occur in the EASTROPAC area belong to the *Lepidophanes*

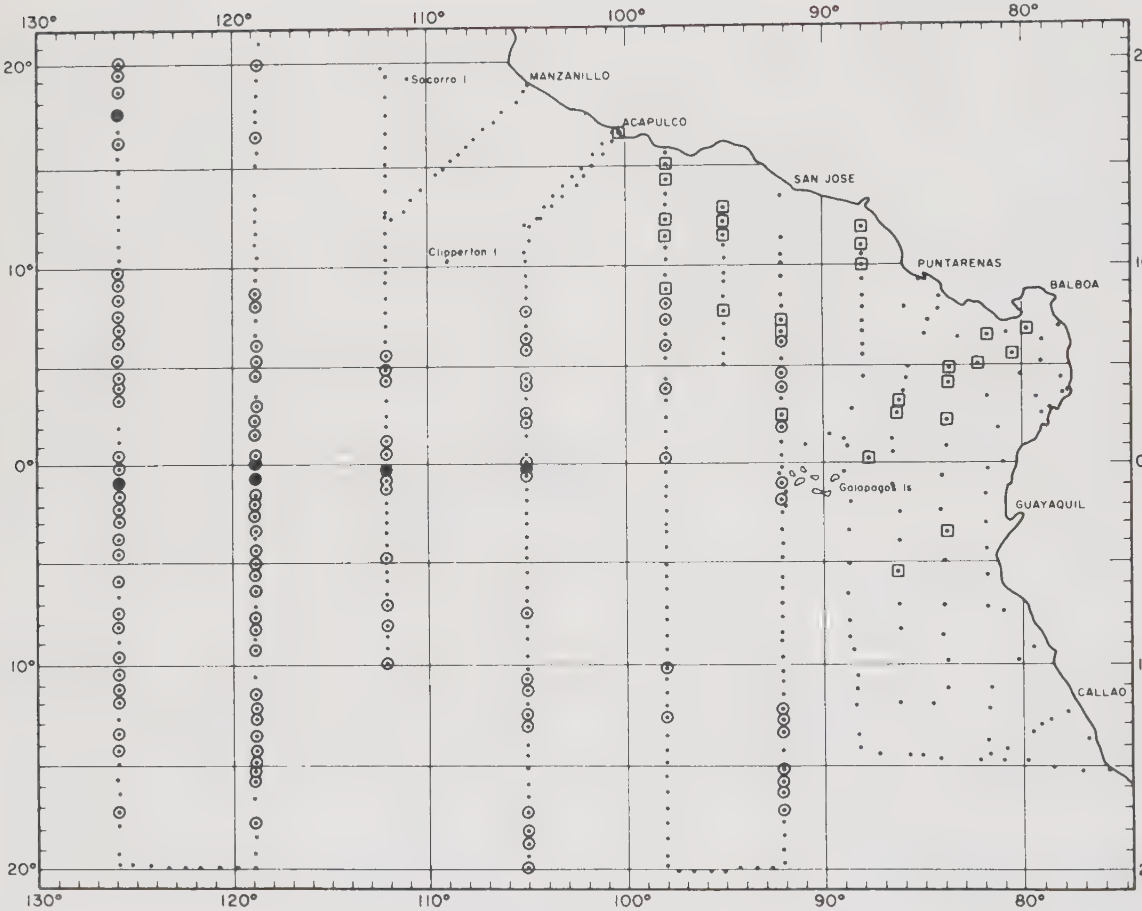

FIGURE 10.—Distribution of larvae of the myctophid *Hygophum proximum* (Becker) and of the bothid flatfish *Bothus leopardinus* (Günther) on EASTROPAC I. Records of occurrence of larvae of *H. proximum* are shown as open circles with dot in center for hauls containing 1 to 25 larvae, and as large solid circles for hauls containing 26 or more larvae; records of occurrence of larvae of *B. leopardinus* are shown as squares; negative hauls are shown as small solid circles.

pyrsobolus (Alcock) complex. Larvae of *Lepidophanes* are almost unpigmented, big eyed, and moderately deep bodied. They have few distinctive characters and can be confused with larvae of *Diaphus* and *Ceratoscopelus*. The majority of the records for *Lepidophanes* were of large larvae.

Lobianchia sp. (16 occurrences, 39 larvae)

Larvae of *Lobianchia* were not recognized until the identification of EASTROPAC larvae was well underway, hence our records of occurrences may be incomplete (some but not all samples were rechecked subsequently). The head of *Lobianchia* larvae is more massive than in most myctophid larvae. The most diagnostic feature, however, is the unusual manner in which the pectoral fins develop: the upper fin rays in each pectoral develop sooner than the remainder of the fin rays and become conspicuously elongated (Tåning, 1918). Twelve of the 16 occurrences were in the pattern worked by *Alaminos* and half of these were at adjacent stations located between lat 6° and 2° N along long 92° W.

Loweina rara (Lutken) (43 occurrences, 56 larvae)

The larger larvae of *Loweina rara* are among the most elegant of myctophid larvae. Larvae of this species were rather uncommon in the EASTROPAC area, although widely distributed. Larvae were taken most frequently, however, in the vicinity of the equator, between ca. lat 8° N and 7° S; 36 of the 43 occurrences were in the equatorial zone. The largest collection of *Loweina* larvae was only four specimens, and only a single specimen was obtained in most collections (i.e., in 35 of 43). The distribution of larvae of *L. rara* on EASTROPAC I is illustrated in Moser and Ahlstrom (1970).

Myctophum spp. (187 occurrences, 1,393 larvae)

Myctophum is one of the more abundant genera represented in the eastern tropical Pacific. Juvenile and adults of five species were obtained in 1-m plankton hauls and micronekton net hauls: *Myctophum aurolaternatum* Garman, *M. asperum* Richardson, *M. brachygnathos* (Bleeker), *M. lychnobium* Bolin, and *M. nitidulum* Garman. Body form and pigmentation of the five of six kinds of *Myctophum* larvae taken in EASTROPAC I are as diverse as has been observed within a myctophid genus. Larvae of *M. nitidulum,* described by Moser and Ahlstrom (1970), are broad headed and deep bodied with eyes on short stalks; larger larvae of this species are among the most heavily pigmented myctophid larvae.

A quite different developmental pattern is displayed by larvae of *M. asperum* and *M. brachygnathos.* The larvae of these species are also deep bodied and big headed, but the eyes are not borne on stalks. The most characteristic feature of the development of these larvae is the early appearance of Dn photophores which form on larvae between 4.0 to 5.0 mm in length, soon after the appearance of the Br_2 photophores. Larvae of *M. asperum* develop large characteristic melanophores (Pertseva-Ostroumova, 1964), but larvae of *M. brachygnathos* are only slightly pigmented.

Larvae of *M. lychnobium* also are but lightly pigmented; they are much more slender and elongated than larvae of *M. brachygnathos* and do not develop the Dn photophores early. A notable feature is the marked length of the teardrop (choroid) tissue that develops under the eyes (as long as in *Gonichthys* or *Centrobranchus* larvae).

The extraordinary larvae of *M. aurolaternatum* were only recently recognized and are not included in the above counts of *Myctophum.*

Notolychnus valdiviae (Brauer) (158 occurrences, 868 larvae)

This is probably the smallest species of myctophid, and certainly one of the most widespread in offshore, oceanic waters. The larvae seldom occur in large numbers (average number per positive haul was 5.5 larvae). They were present in about one-third of the collections made on EASTROPAC I, although most occurrences were farther offshore than 300 miles of the coast (Fig. 11). Juvenile and adult *N. valdiviae* were frequently taken in the oblique plankton hauls. Perhaps as many juvenile and adult specimens of *N. valdiviae* were obtained by this means as of all other myctophids combined. Since this species has only a middling rank with regard to abundance of larvae, the frequency of capture of adults is probably less a measure of abundance than of their shallow depth distribution and poor swimming ability.

Notoscopelus resplendens (Richardson) (70 occurrences, 283 larvae)

This is the species of *Notoscopelus* known to occur in the eastern Pacific. On EASTROPAC, *Notoscopelus* larvae were taken more frequently and in larger numbers in the equatorial zone between lat 5° N and 5° S (40 occurrences, 209 larvae).

Protomyctophum sp. (36 occurrences, 78 larvae)

All occurrences of *Protomyctophum* larvae, except one, were between lat 10° N and 5° S.

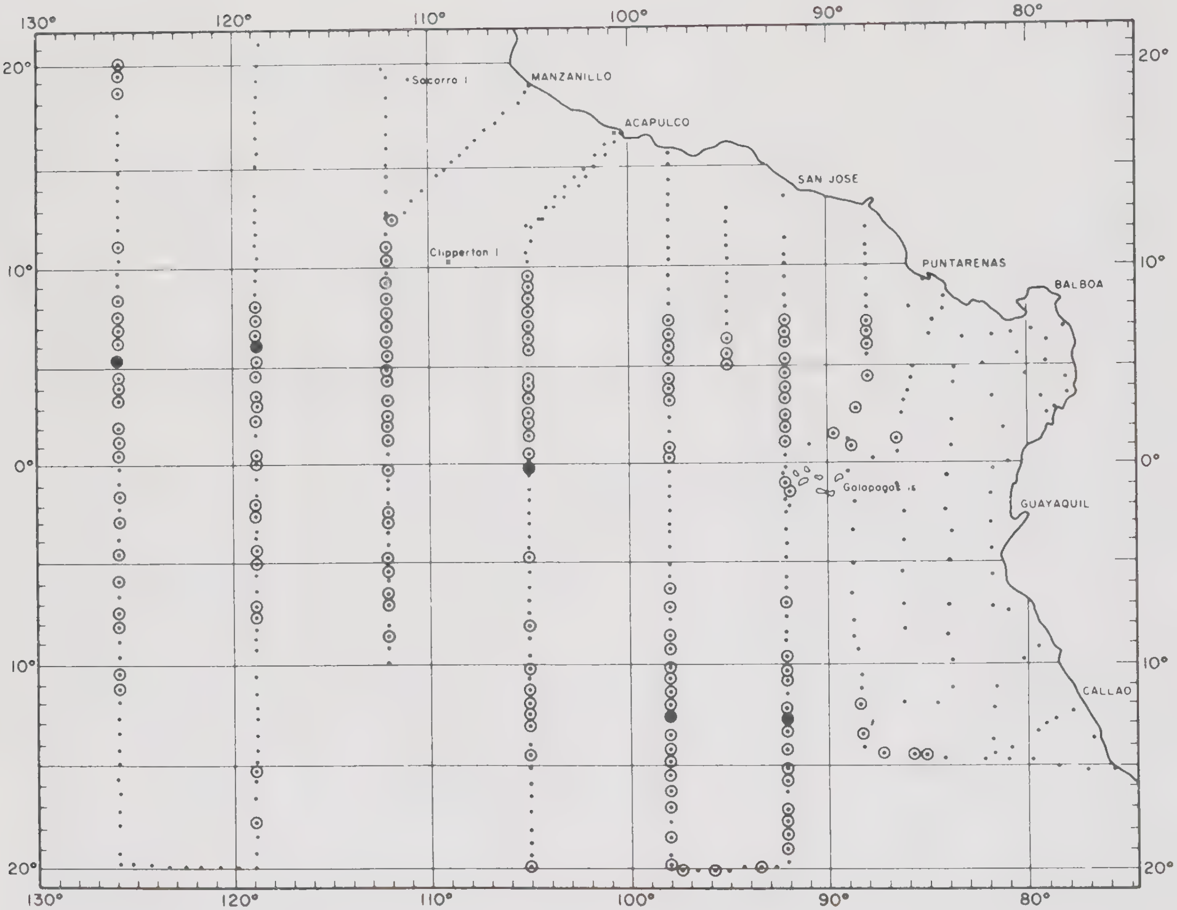

FIGURE 11.—Distribution of larvae of the myctophid, *Notolychnus valdiviae* (Brauer) on EASTROPAC I. Collections of 1 to 25 larvae are shown as circles with dot in center, collections of 26 or more larvae as large solid circles; negative hauls are shown as small solid circles.

Only one kind of *Protomyctophum* larva, belonging to the subgenus *Hierops*, was taken on EASTROPAC. The specific identity is unknown, as no juveniles or adults were obtained. The larva has a single lateral pigment spot per side over the gut, resembling in this respect the larva of *P. crockeri* (Bolin) (Moser and Ahlstrom, 1970). However, internal pigment develops over the hypural bones of the caudal complex in older larvae—resembling in this respect the pigmentation of older larvae of *P. thompsoni* (Chapman). The tropical form lacks ventral pigment on the tail posterior to the anus, such as is developed on larvae of *P. thompsoni*, and probably represents an undescribed species.

Symbolophorus evermanni (Gilbert) (212 occurrences, 1,482 larvae)

Only one kind of *Symbolophorus* larvae appears to be present in the EASTROPAC survey area, despite its distribution in different water masses including the central water mass of the South Pacific. Fewest occurrences were in the northern portion of the EASTROPAC pattern, between lat 10° and 20° N. The number of larvae per positive haul ranged from 1 to 72 (average 7.0); 15 collections contained 25 or more larvae, most distributed between lat 7° and 20° S. Distribution of the larvae of *S. evermanni* on EASTROPAC I is illustrated in Figure 12.

Triphoturus spp. (140 occurrences, 506 larvae)

Larvae of at least two species of *Triphoturus* were taken in the EASTROPAC area. Of particular interest are larvae of *Triphoturus oculeus* (Garman); this species previously was considered a synonym of *T. mexicanus* (Gilbert), but larvae of the two species are differently pigmented. *T. oculeus* occurs in a broad coastal band between Panama and Chile, having in this respect a complementary distribution of that of *T. mexicanus* off California and Baja California.

14. PARALEPIDIDAE

(290 occurrences, 1,648 larvae)

Larvae of Paralepididae were taken in approximately 60 % of the stations occupied on EASTROPAC I. The area of heaviest concentrations was in an equatorial band between lat 5° N and 5° S (Table 16). Two species are

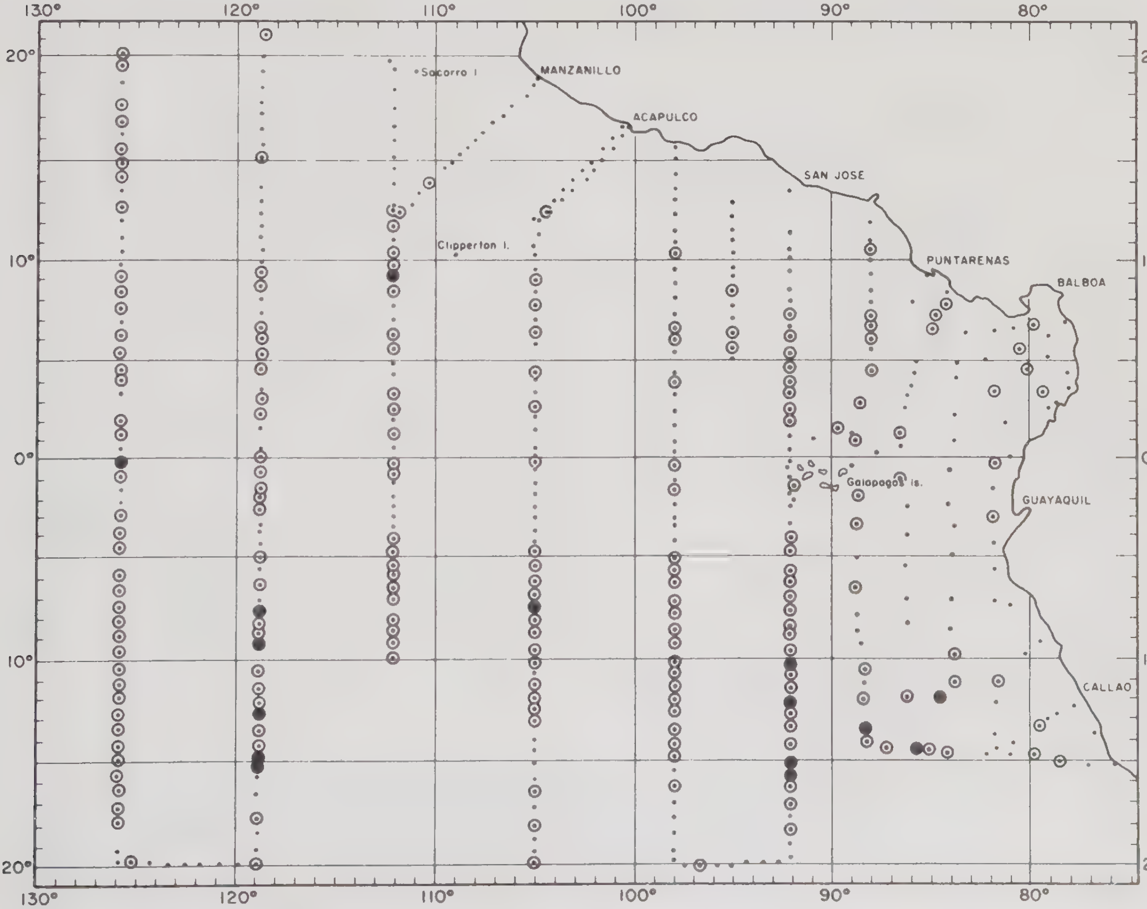

FIGURE 12.—Distribution of larvae of the myctophid, *Symbolophorus evermanni* (Eigenmann and Eigenmann) on EASTROPAC I. Collections of 1 to 25 larvae are shown as large circles with dot in center, collections of 26 or more larvae as large solid circles; negative hauls are shown as small solid circles.

TABLE 16.—Areal occurrence and relative abundance of larvae of Paralepididae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-15° N	7	9	15	63	4	19	--	--	26	91	3.5
15° N-10° N	3	6	22	105	14	77	--	--	39	188	4.8
10° N- 5° N	10	38	10	25	8	39	8	21	36	123	3.4
5° N- 0°	12	83	15	100	11	145	21	219	59	547	9.3
0° - 5° S	8	22	18	217	14	136	11	72	51	447	8.8
5° S-10° S	8	36	7	17	8	62	2	11	25	126	5.0
10° S-15° S	13	32	6	24	9	20	2	2	30	78	2.6
15° S-20° S	6	16	4	7	14	25	--	--	24	48	2.0
Total	67	242	97	558	82	523	44	325	290	1,648	5.7

separately tabulated in Appendix Table 3: *Macroparalepis macrurus* Ege (35 occurrences, 44 larvae), and *Sudis atrox* Rofen (13 occurrences, 15 larvae). These two species have such characteristic larvae that they are readily identifiable. The larvae of *Macroparalepis macrurus* were widely distributed in the EASTROPAC area, except in the inner pattern occupied by *Alaminos* (Fig. 7). In contrast, the larvae of *Sudis atrox* were confined to the central water mass of the South Pacific (Fig. 7). This species was originally described from the central water mass of the North Pacific (Rofen, 1963; see also Berry and Perkins, 1966). Preliminary study of the other paralepidid material indicated that a number of species were represented, but that the most common larva was the form illustrated by Ege (1953, Fig. 27), simply as "*Lestidium* spec."

15. EVERMANNELLIDAE

(27 occurrences, 38 larvae)

The larvae of Evermannellidae in the EASTROPAC area have not yet been worked out in detail. Three species of Evermannellidae are known to occur: *Coccorella atrata* (Alcock), *Evermannella indica* Brauer, and a form with a higher anal fin count than is found in these two species. The identity of the latter, known only as yet from larval specimens, remains uncertain. Although larvae of Evermannellidae were not common, the occurrences were distributed over much of the EASTROPAC pattern, except nearshore.

16. SCOPELARCHIDAE

(142 occurrences, 329 larvae)

Scopelarchids are widely distributed in the eastern tropical Pacific, usually occurring in small numbers, i.e., one to three larvae per haul. Only 15 % of the positive hauls contained larger numbers of larvae, i.e. 4 to 20 larvae per haul. Scopelarchid larvae were most common between lat 10° and 20° N, as is shown in Table 17.

There are at least five species of scopelarchids represented by the larvae, and perhaps six. I have not attempted to attach specific names to most of the kinds because the adult scopelarchids

TABLE 17.—Areal occurrence and relative abundance of larvae of Scopelarchidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-10° N	16	38	25	67	15	84	--	--	56	189	3.4
10° N- 0°	4	4	7	12	10	14	13	27	34	57	1.7
0° -10° S	11	15	9	18	5	8	4	6	29	47	1.6
10° S-20° S	4	7	5	7	9	14	5	8	23	36	1.6
Total	35	64	46	104	39	120	22	41	142	329	2.3

of the eastern tropical Pacific are as yet inadequately known. Most larvae taken between lat 10° and 20° N were those of *Scopelarchoides nicholsi* Parr.

17. SCOPELOSAURIDAE
(9 occurrences, 16 larvae)

Two kinds of *Scopelosaurus* larvae were collected in the EASTROPAC area, but neither has been linked to its adult stages as yet; one of these occurred in only a single collection. Most of the specimens of the other form were taken in an equatorial band, between lat 5° N and 5° S.

20. EEL LEPTOCEPHALI
(87 occurrences, 179 larvae in 1.0-m oblique net hauls; 58 occurrences, 553 larvae in 5.0-ft micronekton net hauls)

A total of 10 families of true eels of the order Anguilliformes, suborder Anguilloidei, is represented in the EASTROPAC I collections. Eel leptocephali were decidedly more common in collections made with the 5-ft micronekton net than in the 1-m net collections: 9.5 larvae per positive haul as compared with 2.1 larvae. This difference probably was due in large part to the larger volume of water strained in taking micronekton net hauls, but the faster towing speed of these hauls, ca. 5 knots as compared with 1.5 to 2 knots for 1-m net hauls, also may have contributed. In the discussion of eel families that follows, I have utilized information on occurrence of eel leptocephali from the collections of both nets.

Congridae

Leptocephali of congrid eels were taken at more stations, 57, than those of any other family, yet no congrid larvae were obtained to the south of lat 6° S. Most congrid leptocephali could be identified to genus, of which five were represented; some larvae, however, could not be identified below the family level. Leptocephali of *Ariosoma* were widely distributed between lat 20° N and 3° S, occurring at 28 stations between the coast and the outer line occupied by *Argo*. Leptocephali of *Hildebrandia* were restricted to a broad coastal band, but leptocephali of *Bathyconger* and *Paraconger* were almost as widespread as those of *Ariosoma*. Only one record was obtained of *Gnathopis*.

Derichthyidae

The only definite record is a metamorphosing specimen obtained at station 11.167.

Moringuidae

Leptocephali of *Neoconger* were taken at five coastal stations between lat 8° N and 1° S.

Muraenesocidae

Leptocephali were taken at four stations in the inner pattern occupied by the *Alaminos*, all within 3° of the equator.

Muraenidae

Muraenid leptocephali were taken at 17 stations; two were on the line of stations occupied off Acapulco, Mexico, and the remainder in the broad corridor between Puntarenas, the Galápagos Islands, and the coast of Ecuador.

Nemichthyidae

Two genera of nemichthyid larvae were represented in the EASTROPAC area, *Nemichthys* and *Borodinula*. A specimen of *Nemichthys*, 310 mm long, was obtained at station 14.188. Leptocephali of this family were taken at 24 stations scattered throughout the EASTROPAC area, including the South Pacific central water mass.

Nettastomidae

Taken at 17 stations in the inner half of the EASTROPAC pattern between lat 9° N and 2° S; two kinds of nettastomid larvae were obtained, one of which was represented by a single specimen.

Ophichthidae

The 31 occurrences of ophichthid eels were distributed in a broad coastal band between Manzanillo, Mexico, and northern Peru (lat 7° S).

Serrivomeridae

Leptocephali of this family were taken at 33 stations, of which 21 were in the outer pattern occupied by *Argo*. Occurrences were grouped into two broad bands—one centered on lat 5° N, the other located between lat 7° and 20° S in the South Pacific central water mass.

Xenocongridae

The leptocephalus of *Chlopsis* was obtained at 22 stations, most located between Panama Bay and the Galápagos Islands.

21. MELAMPHAIDAE

(298 occurrences, 857 larvae)

Melamphaid fishes are the most important family of berycoid fishes in the mesopelagic zone. Four of the five recognized genera occur in the EASTROPAC area: *Melamphaes*, *Scopelogadus*, *Scopelobryx*, and *Poromitra*. According to Ebeling (1962) five species of *Melamphaes* are common in the eastern tropical Pacific, two additional species were collected within the EASTROPAC area, and four other species were collected on the fringes of the area. Only one kind of *Scopelogadus*, *S. mizolepis bispinosus* (Gilbert), is known from the eastern Pacific (Ebeling and Weed, 1963). The remaining two genera, *Scopeloberyx* and *Poromitra*, await revision; the species composition of these genera in the EASTROPAC area is inadequately known. Although melamphaid larvae can be identified to the generic level with some assurance, few developmental series have been worked out at the species level.

Larvae of Melamphaidae were widely distributed in the EASTROPAC area, occurring in 62 % of the collections. Although negative hauls were fewest between the equator and lat 15° N, the average number of larvae per positive haul was rather similar in all areas (Table 18).

23. BREGMACEROTIDAE

(194 occurrences, 1,805 larvae)

Larvae of the gadoid family, Bregmacerotidae, ranked sixth in abundance, contributing 1.9 % of the fish larvae of EASTROPAC I. The only genus, *Bregmaceros*, is widely distributed in pelagic waters of the tropical and subtropical regions of all oceans. D'Ancona and Cavinato (1965) recognized seven species in a worldwide treatment of the genus. These authors stressed the difficulties in species identification.

A preliminary study of EASTROPAC collections of *Bregmaceros* larvae, supplemented by collections of juveniles and adults obtained

TABLE 18.—Areal occurrence and relative abundance of larvae of Melamphaidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20°N-15°N	7	17	15	41	3	5	--	--	25	63	2.5
15° N-10° N	13	36	19	41	18	48	--	--	50	125	2.5
10° N- 5° N	14	59	11	26	24	104	9	24	58	213	3.7
5° N- 0°	7	12	11	19	11	36	24	100	53	167	3.2
0° - 5° S	8	12	9	17	11	56	10	41	38	126	3.3
5° S-10° S	9	18	8	17	9	27	10	21	36	83	2.3
10° S-15° S	6	8	2	6	11	29	6	14	25	57	2.3
15° S-20° S	2	3	2	4	9	16	--	--	13	23	1.7
Total	66	165	77	171	96	321	59	200	298	857	2.9

in micronekton hauls, has shown the presence of five kinds. Larvae of *B. bathymaster* Jordan and Bollman had the most limited distribution, being a coastal species, but were taken in the largest numbers. Two species occurred in the central water mass of the South Pacific (*B. japonicus* Tanaka, and perhaps *B. macclellandi* Thompson). Another species occurred in the equatorial current system, and a fifth species was widely distributed between lat 7° and 20° N. One or both of the latter may be undescribed.

26. EXOCOETIDAE

(78 occurrences, 189 larvae)

The species composition of flyingfish larvae has not been worked out in detail as yet. Only larvae of the most common species, *Oxyporhamphus micropterus* (Cuvier and Valenciennes) (51 occurrences, 121 larvae) have been separately tabulated (Appendix Table 3). Larvae of *Oxyporhamphus* were taken at a number of stations in a coastal band off Mexico and central America. Offshore occurrences were limited to an equatorial band between lat 5° S and 7° N. Only one occurrence of larvae of this species was obtained to the south of lat 5° S. Exocoetid larvae undoubtedly are undersampled in oblique plankton hauls, both because of their shallow depth distribution and their marked swimming ability. Much more material of exocoetids—eggs, larvae, and juveniles—are present in surface plankton hauls; only a few of these have been sorted as yet from EASTROPAC I.

28. GEMPYLIDAE-TRICHIURIDAE

(103 occurrences, 231 larvae)

The larvae of these two families are grouped together for reasons discussed below. Larvae of four species of gempylids-trichiurids appear to be widely distributed in the eastern Pacific: these are *Nealotus tripes* Johnson (42 occurrences, 82 larvae, Fig. 7), *Gempylus serpens* Cuvier and Valenciennes (40 occurrences, 57 larvae, Fig. 13), *Diplospinus multistriatus* Maul (26 occurrences, 62 larvae, Fig. 14), and *Lepidopus* sp. (7 occurrences, 25 larvae, Fig. 14). Records of the occurrence of these in EASTROPAC hauls also are given in Appendix Table 5, and summarized in Table 19. One or two specimens each were taken of larvae of two or three additional species of gempylids-trichiurids.

Late larval stages already have been described for three of the above species (Voss, 1954; Strasburg, 1964), but early developmental stages have not been described, except for a species of *Lepidopus*. We plan to describe the early stage larvae of all the above species.

The larval series of these four species raise questions about the distribution of genera between these two families, and perhaps, about the need for two families. Larvae of *Diplospinus multistriatus* are quite similar to those of *Gempylus serpens*. This similarity is marked enough to have led Voss (1954) to describe the larvae of *Diplospinus* as those of *Gempylus* (*i.e.* her *Gempylus* A). Her *Gempulus* B larvae are those of *Gempylus serpens*.

TABLE 19.—Summary of occurrences and relative abundance of species of Gempylidae-Trichiuridae in the four vessel patterns occupied on EASTROPAC I.

Species	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
Nealotus tripes	6	6	2	7	12	34	22	35	42	82
Gempylus serpens	8	10	15	19	11	18	6	10	40	57
Diplospinus multistriatus	5	10	0	0	9	31	12	21	26	62
Lepidopus sp. (*xantusi*)	0	0	0	0	1	17	6	8	7	25
Other	0	0	2	2	2	3	0	0	4	5
Total	19	26	18	28	31	103	35	74	103	231

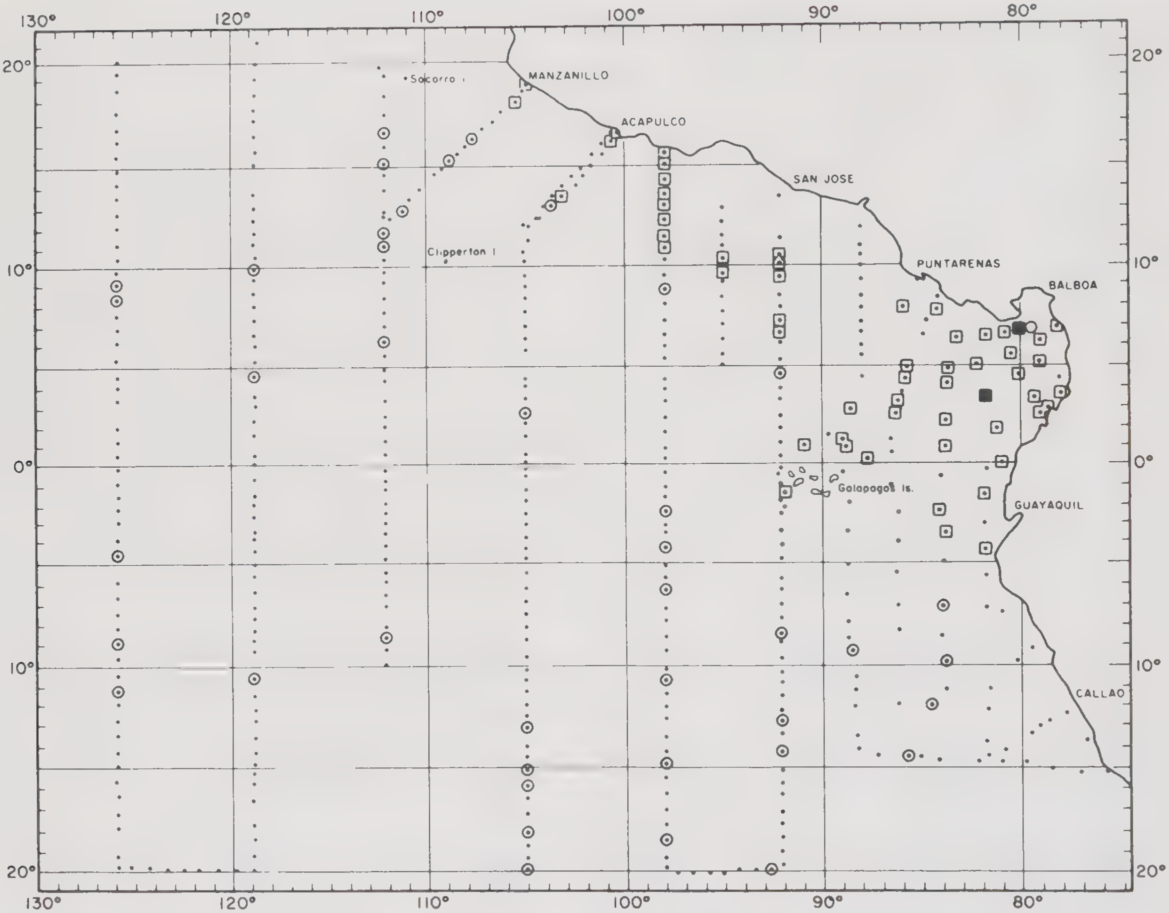

FIGURE 13.—Distribution of larvae of the gempylid, *Gempylus serpens* Cuvier and Valenciennes, and of the cynoglossid flatfish, *Symphurus* spp., on EASTROPAC I. Records of occurrence of larvae of *G. serpens* are shown as large circles with dot in center, *Symphurus* spp. as open squares for hauls containing 1 to 25 larvae and solid squares for hauls with 26 or more larvae; negative hauls are shown as small solid circles.

29. SCOMBRIDAE
(185 occurrences, 1,919 larvae)

Larvae of scombrid fishes ranked fifth in abundance, and made up over 2 % of the larvae. Larvae of the bullet mackerel, *Auxis* spp., (161 occurrences, 1,563 larvae) were by far the most abundant and widely distributed. Larvae of skipjack tuna, *Katsuwonus pelamis* (Linnaeus) (17 occurrences, 214 larvae) were taken mostly in the offshore southern portion of the EASTROPAC area. Other scombrid larvae included yellowfin tuna, *Thunnus albacares* (Bonnaterre) (19 occurrences, 40 larvae); bigeye tuna, *Thunnus obesus* Lowe (1 occurrence, 1 larva); black skipjack, *Euthynnus lineatus* Kishinouye (2 occurrences, 77 larvae); regular *Scomber* sp. (2 occurrences, 7 larvae); Spanish mackerel, *Scomberomorus* sp. (2 occurrences, 3 larvae); and the wahoo, *Acanthocybium solandri* (Cuvier) (1 occurrence, 1 larva). The tuna larvae have been turned over to W. Klawe of the Inter-American Tropical Tuna Commission for detailed study. He kindly has given me permission to include data on occurrence and abundance of larvae of skipjack and bullet mackerel in Ap-

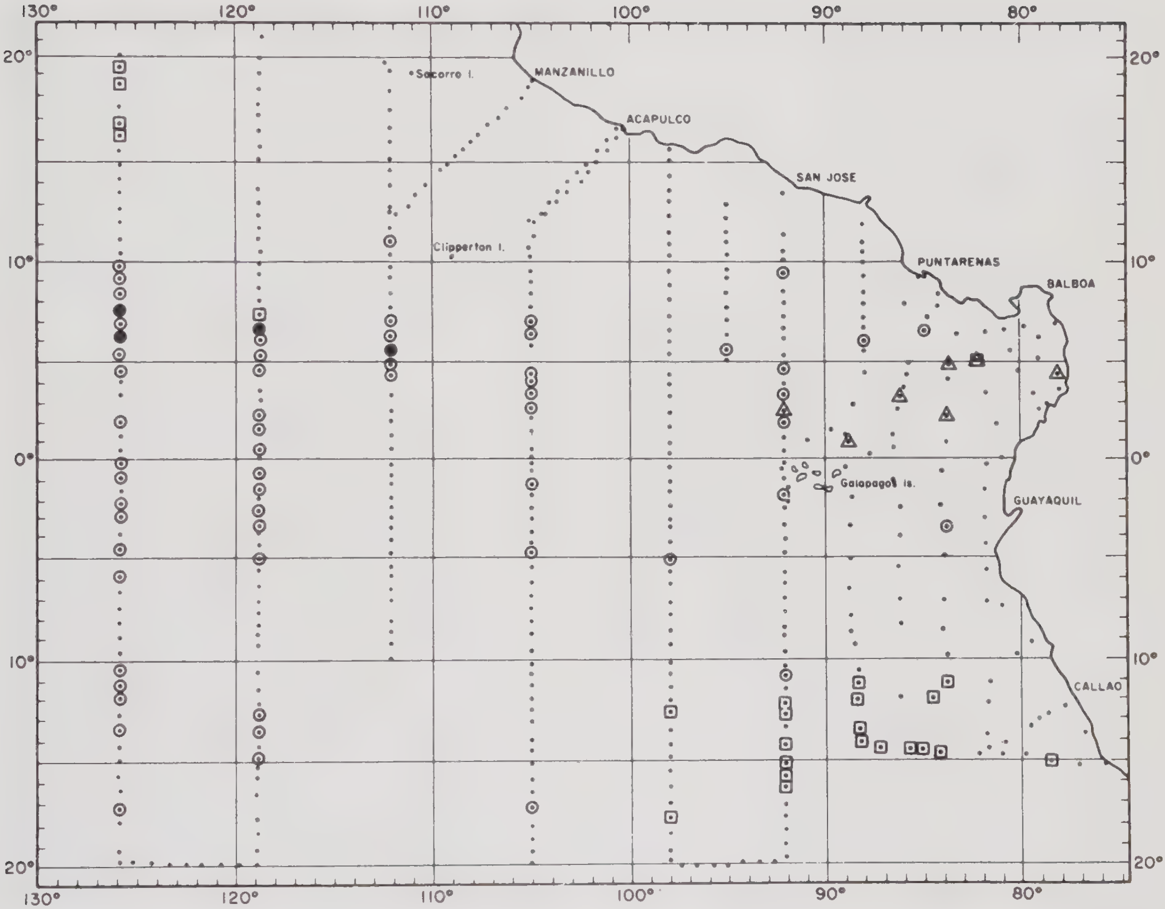

FIGURE 14.—Distribution of larvae of the apogonid, *Howella pammelas* (Heller and Snodgrass), and of the trichiurids, *Diplospinus multistriatus* Maul and *Lepidopus* sp. Records of occurrence of larvae of *H. pammelas* are shown as large circles with dot in center for hauls containing 1 to 10 larvae and large solid circles for hauls containing 11 or more larvae; records of occurrence of larvae of *D. multistriatus* are shown as squares, *Lepidopus* sp. are triangles; negative hauls are shown as small solid circles.

pendix Table 3. Charts showing distribution and relative abundance of larvae of *Auxis* sp. and of *Katsuwonus pelamis* on EASTROPAC cruises will be included in the EASTROPAC Atlas.

30. ISTIOPHORIDAE
(2 occurrences, 2 larvae)

The striking larvae of istiophorids are readily identified to family. The marked paucity of larvae of marlin and sailfish in EASTROPAC I collections was unanticipated, inasmuch as adult billfish are an important part of the Japanese longline catches from the tropical eastern Pacific (Kume and Schaefer, 1966).

32. APOGONIDAE
(61 occurrences, 204 larvae)

Most species of apogonids are coastal, shallow-water forms. A few larvae of these were taken on EASTROPAC I. However, the majority of apogonid larvae were those of *Howella pammelas* (Heller and Snodgrass), a pelagic species that occurred most commonly in the offshore pattern occupied by *Argo* (Fig. 14). An excellent developmental series has been obtained of this species.

36. CARANGIDAE
(31 occurrences, 183 larvae)

Although a number of kinds of carangid larvae were obtained on EASTROPAC I only larvae of the pilotfish, *Naucrates ductor* (L.), are separately tabulated (Appendix Table 3). Most carangid larvae were taken at stations adjacent to the coast or in the vicinity of offshore islands or banks, and over 50 % of the carangid larvae were obtained at two stations (13.019-70 larvae, 14.016-34 larvae). In these larger collections, the most common carangid larvae were *Chloroscombrus orqueta* Jordan and Gilbert and *Selene brevoorti* (Gill). Several times as many young carangids were taken in one haul of the 5-ft micronekton net as in all plankton samples: 384 specimens at station 14.014. Species composition was as follows: *Naucrates ductor*, 288 specimens, 13.0 to 27.5 mm; *Elagatis bipinnulatus* Quoy and Gaimard, 71 specimens, 18.5 to 42.0 mm; and *Caranx caballus* Günther, 25 specimens, 12.0 to 25.0 mm.

40. CORYPHAENIDAE
(86 occurrences, 118 larvae)

Larvae of the dolphin, *Coryphaena* spp., were widely distributed throughout the EASTROPAC area, but occurred in small numbers, usually one or two specimens per positive haul (average 1.4). The occurrence and abundance of *Coryphaena* larvae in various parts of the EASTROPAC area are summarized in Table 20. The majority of specimens obtained were early-stage larvae; no attempt was made to distinguish between the two species of *Coryphaena*. Charts showing distribution of *Coryphaena* larvae on EASTROPAC cruises will be included in the EASTROPAC Atlas.

44. NOMEIDAE
(178 occurrences, 961 specimens)

The nomeids are an important constituent of the epipelagic fauna of the open ocean. Two genera were represented in the EASTROPAC collections, *Psenes* and *Cubiceps*. Larvae of *Cubiceps* were the more common, but more kinds of *Psenes* larvae were obtained. Altogether, eight different kinds of nomeid larvae have been observed, which differ in meristics, pigmentation, and body shape. In several developmental series of larvae of the genus *Psenes* the pelvic fins developed early, and became conspicuously long and pigmented on older larvae. The larger collections of nomeid larvae were obtained between lat 10° N and 5° S (Fig. 15). Only a few collections were obtained to the south of lat 7° S in the patterns occupied by the *Argo*, *Jordan*, and *Rockaway*, i.e. in the central water mass of the South Pacific. Areal occurrences and relative abundance of nomeid larvae on EASTROPAC I are summarized in Table 21.

TABLE 20.—Areal occurrence and relative abundance of larvae of *Coryphaena* spp. on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-10° N	3	4	7	9	6	6	--	--	16	19	1.2
10° N- 0°	14	17	9	17	6	6	9	13	38	53	1.4
0° -10° S	5	6	6	9	4	10	5	7	20	32	1.6
10° S-20° S	2	2	1	1	3	3	6	8	12	14	1.2
Total	24	29	23	36	19	25	20	28	86	118	1.4

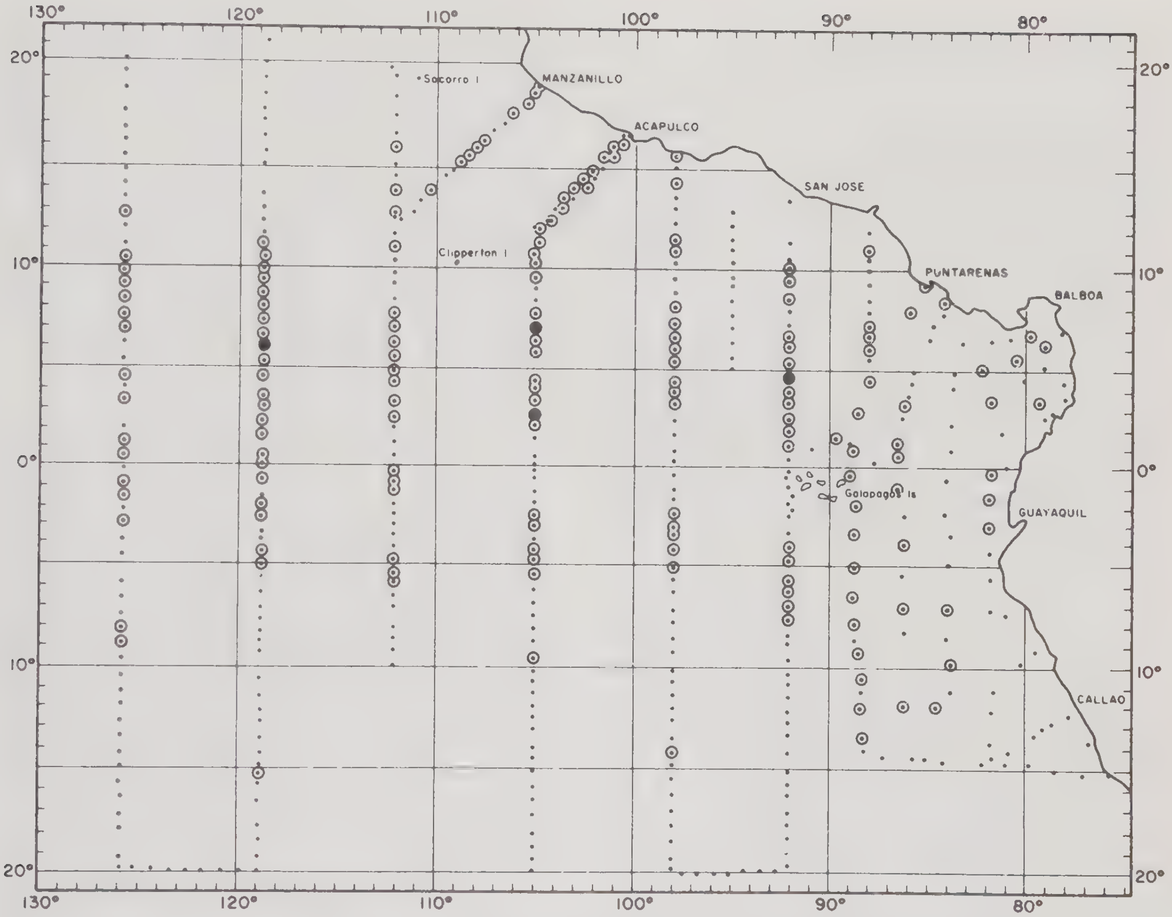
130°
120°
110°
100°
90°
80°
20°
10°
0°
10°
20°
Socorro I
MANZANILLO
ACAPULCO
SAN JOSE
Clipperton I
PUNTARENAS
BALBOA
Galapagos Is
GUAYAQUIL
CALLAO

FIGURE 15.—Distribution of larvae of the family Nomeidae on EASTROPAC I. Collections of 1 to 25 larvae are shown as large circles with dot in center, of 26 or more larvae as large solid circles; negative hauls are shown as small solid circles.

TABLE 21.—Areal occurrence and relative abundance of larvae of Nomeidae on EASTROPAC I.

Latitude	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I		
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	Average no. larvae per positive haul
20° N-15° N	0	0	11	39	3	7	--	--	14	46	3.3
15° N-10° N	5	12	11	24	10	26	--	--	26	62	2.4
10° N- 5° N	12	81	9	87	17	87	7	21	45	276	6.1
5° N- 0°	11	46	9	130	9	76	9	39	38	291	7.7
0° - 5° S	8	26	8	60	6	78	8	30	30	194	6.5
5° S-10° S	2	3	4	6	5	16	7	44	18	69	3.8
10° S-15° S	0	0	0	0	1	1	5	12	6	13	2.2
15° S-20° S	1	10	0	0	0	0	--	--	1	10	10.0
Total	39	178	52	346	51	291	36	146	178	961	5.4

51. TETRAGONURIDAE
(6 occurrences, 7 specimens)

Only a few specimens of *Tetragonurus* larvae were obtained in EASTROPAC I collections. Larvae of *Tetragonurus* have been taken rather commonly in the California Current region and were an important constituent in NORPAC collections. These interesting oceanic fishes were revised by Grey (1955), who recognized three species. Two of these were present in the EASTROPAC area: *T. atlanticus* Lowe and *T. cuvieri* Risso. Late-stage larvae of the two species can be separated by differences in their meristics, and also by differences in pigmentation and body form; larvae of *T. atlanticus* are more heavily and uniformly pigmented and are deeper bodied than larvae of *T. cuvieri* (Grey, 1955).

PLEURONECTIFORMES
(79 occurrences, 503 larvae)

Larvae of flatfishes (Pleuronectiformes) in EASTROPAC collections belonged only to the families Bothidae and Cynoglossidae. Information concerning the kinds and numbers of flatfish larvae taken at each of 79 EASTROPAC I stations is contained in Appendix Table 6; this information is summarized in Table 22.

Flatfish larvae were taken in a broad coastal band, several hundred miles wide, between Manzanillo, Mexico, and northern Peru. The occurrences of some kinds of flatfish larvae and juveniles at considerable distances from shore have been commented upon by a number of workers. Kyle (1913) obtained larvae of *Bothus* from across the North Atlantic and larvae of *Syacium* at considerable distances from shore. Bruun (1937a, 1937b) described bathypelagic occurrences of the bothid flatfish, *Chascanopsetta* and *Monolene*, the latter from off Panama, and of the pleuronectid flatfish, *Poecilopsetta*. Ahlstrom (1965) illustrated the widespread offshore distribution of larvae of *Citharichthys* spp. in the California Current region.

54. BOTHIDAE
(56 occurrences, 199 larvae)

Several kinds of bothid flatfish larvae were taken in 20 or more collections, including larvae of *Bothus leopardinus* (Günther), *Syacium ovale*, and *Citharichthys-Etropus*. Some interesting forms taken less frequently included larvae of *Cyclopsetta* sp., *Engyophrys sancti-laurentii* Jordan and Bollman, and of *Monolene*. A short section will be devoted to each of the above.

Bothus leopardinus (Günther) (28 occurrences, 50 larvae)

Although Norman (1934) lists three species of *Bothus* as occurring in the eastern tropical Pacific—*Bothus mancus* (Broussonet), *B. leop-*

TABLE 22.—Frequency of occurrence and relative abundance of the principal kinds of flatfish larvae, Pleuronectiformes, on EASTROPAC I, summarized by vessel pattern.

Flatfish larvae	*Argo* 11.000 series		*David Starr Jordan* 12.000 series		*Rockaway* 13.000 series		*Alaminos* 14.000 series		Total EASTROPAC I	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
BOTHIDAE										
Bothus leopardinus	0	0	1	4	15	32	12	14	28	50
Citharichthys-Etropus	0	0	2	2	6	8	18	40	26	50
Cyclopsetta sp.	0	0	0	0	2	2	1	2	3	4
Engyophrys sancti-laurentii	0	0	0	0	2	3	6	6	8	9
Syacium ovale	0	0	2	8	13	60	9	16	24	84
Other Bothidae	0	0	0	0	1	1	1	1	2	2
Total Bothidae	0	0	3	14	24	106	29	79	56	199
CYNOGLOSSIDAE										
Symphurus spp.	0	0	5	17	21	102	37	185	63	304
Total Pleuronectiformes	0	0	6	31	30	208	43	264	79	503

pardinus (Günther), and *B. constellatus* (Jordan)—he notes that the latter is very doubtfully distinct from *B. leopardinus.* Based on larval material, there appears to be only one common, widely distributed species in the eastern Pacific (Fig. 10), which is referred to *B. leopardinus.* It lacks pigmentation, except for a dorsal and ventral finfold spot near the end of the notochord. This finfold pigment has been observed on a number of species of *Bothus,* hence may be a generic character. *Bothus* larvae are readily separable from other bothid flatfish larvae in the EASTROPAC area by a number of characteristics. Young-stage larvae possess a single elongated anterior dorsal ray, which becomes inconspicuous in older larvae. Older larvae are very deep bodied, usually lack pigmentation and lack head spination. The pelvic fin base on the left side originates mostly anterior to the cleithrum, not posterior as in *Syacium, Engyophrys, Cyclopsetta,* or *Citharichthys,* and the fin on the ventral midline is much broader based than in these genera. Almost 100 specimens of *Bothus* larvae from the tropical eastern Pacific have been cleared and stained (based in part on EASTROPAC material, in part on previous expeditions). The modal number of vertebrae was 10 + 28 = 38.

Several specimens of flatfish larvae were taken on EASTROPAC I, and on previous expeditions, that had an exceptionally heavy, elongated, single anterior dorsal ray, such as have been described for several genera of bothid flatfish of the subfamily Bothinae. However, the pelvic fins formed behind the cleithrum and the fin on the ventral margin was not much wider based than its recessed partner. These intriguing larvae appear to be those of *Monolene.* Two different kinds have been obtained from the eastern tropical Pacific, one form has 10 + 35 vertebrae, the other has 10 + 28 vertebrae. The latter may be the larva of *Monolene asaedai* (Perkins, 1963).

Cyclopsetta sp. (3 occurrences, 4 specimens)

Larvae of *Cyclopsetta* are more closely related to those of *Syacium* than to other bothid genera. Larvae of both genera develop marked opercular spination as well as a sphenotic spine on either side of the head. *Cyclopsetta* larvae develop 8 to 11 elongated anterior dorsal rays, rather than 5 to 8 as in *Syacium. Cyclopsetta* larvae also attain a larger size before transformation; larval specimens as large as 32 mm have been observed in the EASTROPAC area. In late-stage larvae of *Cyclopsetta* the anterior group of dorsal rays is quite elongated, but a more striking feature is the marked development of three rays of the left pelvic fin which may extend almost to the base of the caudal fin. The *Cyclopsetta* larvae have a larger number of vertebrae—usually 10 + 29, as compared to 10 + 25 for larvae of *Syacium ovale* (Günther). Three species of *Cyclopsetta* have been described from the tropical eastern Pacific—*C. querna* (Jordan and Bollman), *C. panamensis* (Steindachner), and *C. maculifera* (Garman), but only *C. querna* has been collected with any frequency as juveniles and adults. The usual count of vertebrae in *C. querna* and *C. panamensis* is 10 + 29; the vertebral count of *C. maculifera* is not known.

Engyrophrys sancti-laurentii Jordan and Bollman (8 occurrences, 9 larvae)

Larvae of *Engyophrys* are about as deep bodied as those of *Bothus.* They possess heavy serrations on the ventral edge of the body both fore and aft of the cleithrum; three small spines also develop on the otic region of the head. The pelvic fins develop immediately posterior to the cleithrum and anterior to the posterior group of ventral serrations. A cleared and stained specimen, 18 mm long, from station 13.040 had 10 + 31 vertebrae, 86 dorsal rays, 71 anal rays, and 17 caudal rays.

Syacium ovale (Günther) (24 occurrences, 84 larvae)

A larval stage of *Syacium* was first illustrated by Kyle (1913) as "*Ancylopsetta* sp." *Syacium* has a distinctive larva with heavy opercular spination, a sphenotic spine on either side of the head, and 5 to 8 elongated anterior dorsal rays. Larvae of the closely related genus, *Cyclopsetta,* also develop opercular and head spination. The opercular spination is more pronounced in *Syacium*—particularly an antlerlike spine that develops on the posterior border of the preoperculum. The three anterior rays of the left pelvic fin become only moderately elongated in *Syacium* larvae; the rays are of about equal length, firmly joined together by a membrane, and pigmented distally. The full complement of dorsal and anal fin rays usually are laid down before the larvae attain a standard length of 10 mm; the largest specimens studied, ca. 20 mm long, were undergoing metamorphosis.

Citharichthys-Etropus (26 occurrences, 50 larvae)

Before discussing problems in identification of *Citharichthys-Etropus* larvae from the EASTROPAC area, some background information will be given on *Citharichthys* larvae in the CalCOFI region. Illustrations of larvae of three species of *Citharichthys* were given in Ahlstrom (1965). Two species, *Citharichthys sordidus* (Girard) and *C. xanthostigma* Gilbert, develop 2 elongated dorsal rays and also 2 elongated ventral rays on larvae larger than about 5 mm; the other species never develops such rays. Another species that occurs off central and southern Baja California, *C. fragilis* Gilbert, also develops 2 elongated rays on the dorsal and ventral fins.

Two species of *Citharichthys, C. gilberti* Jenkins and Evermann, and *C. platophrys* Gilbert, and the widely distributed *Etropus crossotus* Jordan and Gilbert are known to occur in the EASTROPAC area. Three kinds of larvae were taken in EASTROPAC collections referable to *Citharichthys* or *Etropus.* The most common kind developed 3 elongated dorsal rays, a less common form developed 2 elongated dorsal rays, and some specimens lacked elongated rays. The form with 3 elongated dorsal rays is almost certainly referable to *Citharichthys.* Larvae of a common Atlantic species, *C. arctifrons* Goode, develop 3 elongated dorsal rays, confirming the presence of this combination in *Citharichthys* larvae. A cleared and stained specimen from station 13.040 with 3 elongated dorsal rays possessed 10 + 25 vertebrae, 78 dorsal rays, and 59 anal rays. The meristics of the dorsal and anal fins could fit either *C. platophrys* or *C. gilberti.* Yet so little is known of *C. platophrys* that I would hesitate to refer the common *Citharichthys* larvae in EASTROPAC material to this species. A similar problem attends larvae of the form that lacks elongated dorsal rays. Two specimens, 11.5 and 12.0 mm, from station 14.014 each had 88 dorsal and 67 anal rays; vertebrae counts were 10 + 23 and 10 + 24. These counts best fit *E. crossotus,* except that the vertebral counts are low. No material of the form with 2 dorsal rays (undoubtedly a *Citharichthys*) has been cleared and stained for precise meristics. A definite identification has yet to be made on all three kinds of larvae.

55. CYNOGLOSSIDAE
(63 occurrences, 304 larvae)

Only one cynoglossid genus, *Symphurus,* occurs in the eastern Pacific. Five or more kinds of *Symphurus* larvae were obtained in EASTROPAC collections; these were obtained in more collections than larvae of bothid flatfishes (63 as compared with 56), and made up a larger percentage of the total flatfish larvae (ca. 60 %). A moderate number of recently transformed specimens of *Symphurus* were obtained in EASTROPAC collections; in contrast, all specimens of bothid flatfish were pretransformation larvae. The distribution of *Symphurus* larvae in EASTROPAC I is shown in Figure 13.

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APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
11.022	0	10	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
.025	0	52	0	0	0	0	0	11	1	3	0	0	0	0	0	0	0	0	0	0	2	0	69
.027	0	36	0	0	0	4	0	14	1	0	0	0	0	0	0	0	0	0	0	1	0	1	57
.030	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
.032	1	15	0	0	0	0	0	19	0	0	0	0	2	0	0	0	0	0	0	0	2	1	40
.034	1	88	0	0	0	1	0	35	0	0	0	0	0	0	0	0	0	0	0	0	1	2	128
.036	0	26	0	0	0	0	1	3	1	0	0	0	3	0	0	0	0	0	0	0	0	0	34
.038	4	22	0	0	0	4	0	21	2	0	0	0	6	0	0	0	0	0	0	0	1	0	60
.040	0	20	0	0	0	11	0	55	0	3	0	3	3	0	0	0	0	0	0	4	1	0	100
.044	2	9	0	0	0	20	0	5	1	0	0	2	4	0	0	0	0	0	0	0	3	0	46
.046	3	58	0	0	0	22	0	50	0	4	0	1	2	0	0	0	0	0	1	1	1	3	146
.048	12	41	0	0	0	12	0	20	3	1	0	3	1	0	0	0	0	0	0	0	0	1	94
.050	24	23	0	0	0	3	1	36	0	1	0	2	0	0	0	0	0	0	0	0	1	10	101
.052	15	3	15	0	0	2	0	58	0	0	0	4	2	0	0	0	1	1	0	0	0	1	102
.054	11	8	17	0	0	0	0	159	0	1	0	2	0	0	0	0	3	0	0	0	0	4	205
.056	10	8	0	0	0	0	0	67	0	5	0	0	0	0	0	1	5	0	0	0	5	12	113
.058	10	3	14	0	0	0	0	28	0	0	0	6	2	0	0	0	1	0	0	1	1	10	76
.060	13	9	30	2	1	0	0	72	2	0	0	2	0	0	3	0	5	0	0	2	5	1	147
.062	0	0	6	0	0	0	0	21	2	0	0	5	1	0	0	0	1	0	0	0	1	3	40
.064	0	1	22	0	0	0	2	51	0	0	0	3	3	0	0	1	7	2	0	2	3	2	99
.066	0	2	16	1	0	0	0	63	4	0	0	1	7	3	3	0	4	2	0	15	0	5	126
.068	5	77	49	0	2	0	3	229	4	0	3	6	45	1	2	0	26	1	1	10	9	0	473
.070	1	24	21	0	5	1	0	96	6	0	3	1	25	1	0	0	9	1	0	12	8	9	223
.072	2	73	20	0	6	1	4	178	4	0	1	2	11	0	0	1	16	1	0	12	8	0	340
.076	6	689	21	0	5	4	3	90	0	1	0	2	0	0	4	0	2	0	0	4	7	20	858
.080	7	142	11	0	0	0	6	36	3	0	0	2	1	0	0	0	4	0	0	0	7	0	219
.084	11	361	3	0	1	1	0	131	6	1	0	0	1	0	4	0	3	0	1	2	0	26	552
.088	1	324	3	0	0	0	1	104	3	1	0	0	0	0	0	0	7	0	0	3	0	8	455
.094	0	50	2	0	1	0	0	66	14	0	0	0	0	0	0	0	1	0	0	5	4	4	147
.098	2	107	2	0	0	0	0	907	20	0	0	2	1	0	1	0	4	0	23	12	4	12	1097
11.102	6	33	4	0	0	0	0	99	7	0	0	0	0	0	0	0	1	0	0	12	1	5	168
.106	1	10	2	0	1	0	2	22	0	0	1	0	0	0	0	0	0	2	0	6	0	1	48
.110	8	9	7	0	0	0	0	57	0	1	0	0	0	0	0	0	1	0	0	0	3	1	87
.114	1	57	43	0	0	0	1	243	1	0	0	1	0	0	0	1	3	0	0	5	1	1	358
.118	4	7	6	0	0	0	0	84	0	0	0	3	0	0	0	0	0	1	0	2	2	3	112
.120	1	3	2	0	0	0	0	9	0	0	0	1	0	0	0	0	0	0	1	2	3	0	22
.124	0	25	11	0	0	0	0	66	0	0	0	0	0	0	1	0	5	0	0	0	0	3	111
.128	0	98	6	0	0	0	2	98	4	1	0	1	0	0	0	0	10	1	0	3	4	2	230
.130	0	7	6	0	2	0	1	29	2	0	0	0	0	0	0	0	0	1	0	0	3	0	51
.132	0	8	4	0	1	1	5	16	0	0	0	0	0	0	0	0	0	2	0	1	4	0	42
.134	0	28	0	0	0	0	2	109	4	0	0	1	0	4	171	0	0	0	0	3	8	4	334
.136	0	46	33	0	0	2	2	168	9	2	6	4	0	0	2	0	0	0	0	0	7	1	282
.138	0	8	34	0	0	0	5	21	4	0	0	2	6	0	0	1	0	3	0	2	1	0	87
.140	0	5	9	0	0	0	0	12	0	2	2	0	0	0	0	1	0	0	0	0	1	1	33
.142	0	13	7	0	0	0	0	69	8	1	0	1	1	0	0	0	0	0	1	2	0	7	110
.146	0	22	3	0	0	0	0	17	0	0	0	0	0	0	3	1	0	0	0	0	0	3	49
.148	0	77	2	0	0	0	0	13	1	0	0	1	1	0	0	0	0	0	0	0	2	6	103
.150	0	82	2	0	0	1	2	38	2	0	0	0	0	0	4	0	0	0	0	0	0	10	141
.152	0	138	4	0	0	0	1	115	3	0	0	0	1	0	1	0	0	0	0	4	1	0	268
.154	0	8	4	0	0	2	0	15	1	0	0	2	1	0	0	0	0	0	0	5	0	7	45
.156	0	88	3	0	0	0	2	29	4	0	0	2	2	0	0	0	0	0	0	1	5	21	157
.158	0	40	2	0	1	6	0	103	6	0	0	1	3	0	0	1	0	1	0	4	2	29	199
.159	0	102	2	0	0	1	1	117	9	0	1	2	0	1	0	1	10	4	0	3	5	27	286
.161	0	12	3	0	0	1	0	10	0	0	0	0	2	0	0	0	0	0	0	1	0	2	31

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
11.163	0	8	1	0	0	0	2	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	14
.167	0	30	0	0	0	0	1	20	1	0	0	0	0	0	1	0	0	0	0	0	3	0	56
.169	0	4	1	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	9
.171	0	11	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	13
.173	0	9	0	0	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	1	0	0	16
.175	0	2	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	1	0	0	8
.177	0	5	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	2	0	1	11
.179	0	5	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	1	0	0	19
.181	0	13	3	0	0	0	0	13	1	0	0	0	0	0	0	0	0	0	0	1	0	0	31
.183	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	8
.185	0	5	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
.187	0	22	1	0	0	0	1	24	0	1	0	0	0	1	0	0	0	0	0	1	0	1	52
.189	0	21	1	0	0	0	0	19	0	0	0	0	0	0	0	0	0	1	0	0	0	1	43
.191	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4
.195	0	14	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
.197	0	45	1	0	0	0	1	60	3	0	0	0	1	0	2	0	0	0	0	6	0	5	124
.199	0	6	0	0	0	1	0	9	0	0	0	1	0	0	1	0	0	0	0	3	0	5	26
11.201	0	2	2	0	0	0	0	8	0	0	1	0	1	0	0	0	0	0	0	1	0	0	15
.203	0	24	1	0	0	0	0	17	1	0	0	0	1	0	0	0	0	0	0	2	0	4	50
.205	0	53	1	0	0	1	3	40	2	0	0	0	7	0	0	0	0	0	0	0	0	5	112
.207	0	15	0	0	0	1	0	21	2	0	0	0	0	0	0	0	0	0	0	1	0	7	47
.209	0	7	1	0	0	1	0	12	2	3	0	1	4	0	0	0	0	0	0	2	1	2	36
.211	0	39	5	0	0	0	1	28	1	0	0	1	1	0	0	0	0	0	0	2	6	5	89
.213	0	37	5	0	0	0	3	71	3	2	0	0	3	0	4	1	0	0	0	2	4	1	136
.215	0	5	7	0	0	0	0	44	4	0	0	0	6	0	3	0	0	0	0	2	4	5	80
.217	0	8	7	0	0	0	1	16	0	0	0	1	4	0	0	0	0	1	0	3	0	1	42
.219	0	2	15	0	0	0	0	10	1	0	0	0	6	0	1	1	1	0	0	0	2	1	40
.221	0	56	35	0	0	0	0	74	6	2	3	2	6	0	1	0	2	2	0	1	3	1	194
.223	0	13	32	1	0	0	0	20	0	0	1	3	5	0	0	0	0	0	0	0	0	1	76
.226	0	5	4	0	0	1	0	7	0	1	3	1	3	0	0	0	0	0	0	0	0	0	25
.228	0	3	12	1	0	2	0	16	2	0	2	3	4	0	0	1	0	0	0	1	4	3	54
.234	2	17	19	0	0	0	0	46	1	2	0	1	0	0	0	1	0	0	0	6	5	17	117
.238	0	8	7	0	1	0	1	10	0	0	0	1	0	0	0	0	0	2	0	1	0	13	44
.242	4	50	20	1	1	0	0	95	1	1	0	2	0	1	0	0	2	2	1	5	3	6	195
.246	2	52	6	0	4	0	0	198	1	1	0	0	0	0	0	0	0	1	0	4	3	2	274
.250	1	20	6	0	0	0	0	57	1	0	0	2	0	0	0	0	2	0	0	6	0	5	100
.254	0	20	1	0	0	0	2	149	6	1	0	0	0	2	0	0	2	0	7	2	8	23	223
.258	3	54	6	0	0	0	0	108	9	0	0	2	0	0	0	0	0	0	0	2	3	2	189
.262	2	68	1	0	0	0	3	85	9	0	0	0	0	0	0	0	2	0	0	0	2	3	175
.266	3	33	5	0	0	0	0	38	1	0	0	0	0	0	0	0	5	0	0	0	4	0	89
.270	4	19	8	0	0	0	0	17	0	0	0	0	0	0	7	0	0	0	0	1	6	4	66
.278	13	155	13	0	0	1	0	116	3	0	1	1	4	0	0	0	1	0	0	2	4	3	317
.282	1	27	4	0	1	1	1	82	6	0	5	0	7	0	0	0	0	3	1	3	5	4	151
.285	9	10	34	0	0	1	1	30	5	0	3	1	13	1	0	0	1	0	0	5	3	25	142
.287	1	18	13	0	0	3	2	87	8	1	4	5	13	0	0	0	0	0	0	5	5	7	172
.289	0	17	18	0	0	4	1	131	2	0	3	10	6	0	0	0	0	0	0	25	2	10	229
.291	0	2	19	0	0	1	0	39	0	0	2	6	10	0	0	0	1	0	0	5	0	6	91
.293	7	3	46	0	0	1	1	50	2	0	1	5	5	0	6	0	9	3	1	16	2	8	166
.295	10	15	40	0	0	0	0	130	4	0	0	4	0	0	1	2	12	1	0	7	3	3	232
.297	5	12	3	0	0	0	0	297	4	0	0	1	4	0	3	2	2	0	1	5	1	9	349
.299	27	2	15	0	0	0	0	29	0	0	0	4	0	0	5	0	4	1	0	4	0	2	93
11.301	1	13	0	0	0	6	0	8	0	1	0	2	1	0	2	0	2	1	0	4	0	3	44
.303	12	47	0	0	1	8	0	44	0	0	0	4	1	0	0	0	0	1	0	2	0	7	127
.306	4	64	0	0	0	3	0	40	0	0	0	4	1	0	1	0	0	0	1	1	0	4	123

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
11.308	1	6	2	0	1	0	0	13	0	1	0	2	8	0	0	0	1	0	1	3	0	5	44
.310	4	6	2	0	1	0	0	15	0	1	0	6	10	0	0	0	0	0	1	2	2	3	53
.312	0	62	3	0	0	0	0	26	2	0	0	3	1	0	0	0	0	0	0	2	0	1	100
.314	5	32	2	0	0	1	1	27	0	1	0	1	0	0	0	0	0	1	0	1	1	1	74
.316	0	3	3	0	0	0	1	8	0	0	0	3	2	0	0	0	0	3	0	2	1	0	26
.318	0	3	13	0	0	0	0	34	0	1	0	1	2	0	0	5	0	0	0	1	0	1	61
.320	1	10	5	0	0	2	0	11	1	0	0	0	2	0	0	1	0	0	0	1	0	6	40
.322	0	35	11	0	0	2	1	115	0	10	0	3	1	0	0	0	0	0	0	1	1	6	186
.324	0	21	1	0	1	1	0	13	1	1	0	1	4	0	0	1	0	0	0	0	0	3	48
.326	0	36	3	0	0	1	1	31	0	1	0	1	4	0	0	2	0	0	0	0	0	1	81
.328	0	40	7	0	0	4	1	55	2	3	0	5	2	0	0	0	0	0	0	0	0	3	122
12.002	3	13	0	0	0	21	1	37	1	4	0	2	0	0	0	0	0	0	0	0	0	1	83
.004	3	12	0	0	0	32	3	85	1	2	0	3	3	0	0	1	0	0	0	4	0	3	152
.006	2	15	1	0	1	29	5	33	5	1	0	2	2	0	0	0	0	0	1	24	0	2	123
.008	3	65	0	0	0	17	2	88	1	9	0	0	1	0	0	0	2	0	0	12	0	3	203
.010	8	98	0	0	0	22	0	121	1	1	0	7	2	0	0	0	0	0	0	6	1	2	269
.012	4	24	0	0	0	10	1	31	6	1	0	1	1	0	0	0	0	1	0	8	0	2	90
.014	4	38	0	0	0	8	2	23	5	0	0	4	1	0	0	1	3	0	0	8	0	9	106
.016	8	182	0	0	0	10	4	69	6	4	0	2	1	0	1	0	3	0	0	9	0	2	301
.018	0	199	0	0	0	10	7	137	3	2	0	2	1	1	0	0	1	0	0	7	0	0	370
.020	3	23	0	0	0	5	4	74	4	0	0	4	1	0	0	1	2	0	0	4	1	1	127
.022	0	21	0	0	0	0	1	16	6	0	0	0	1	1	0	0	0	0	0	5	0	5	56
.024	3	242	0	0	0	0	32	97	6	0	0	1	0	0	0	0	0	0	0	13	1	5	400
.026	4	101	0	0	0	1	3	121	6	3	0	4	1	0	0	0	3	0	2	19	0	0	268
.028	0	32	0	0	0	0	3	13	3	0	0	4	0	2	3	0	3	0	0	8	2	0	73
.030	6	12	0	0	0	1	0	24	3	0	0	0	6	0	1	0	14	0	0	7	1	3	78
.032	0	13	0	0	0	0	1	20	2	0	1	1	12	0	7	0	3	0	1	23	0	314	398
.033	3	36	0	0	0	2	4	87	5	1	2	2	533	0	6	0	0	0	0	38	5	4	728
.035	1	73	0	0	0	0	4	23	2	1	0	1	70	5	2	0	4	0	1	18	0	3	208
.037	9	11	0	0	0	3	1	36	3	1	0	0	2	0	3	0	2	0	0	0	0	0	71
.039	4	3	0	0	0	10	0	17	2	3	1	1	5	3	0	0	0	0	0	0	0	1	50
.041	3	22	0	0	0	6	3	108	4	1	2	1	3	3	1	0	0	0	0	8	0	2	167
.043	0	28	0	0	0	16	2	94	22	2	0	1	16	6	1	0	1	0	0	4	0	7	200
.045	0	7	0	0	0	4	0	33	2	2	0	1	5	3	0	0	0	0	0	3	0	3	63
.047	1	4	0	0	0	4	0	61	5	2	0	1	21	4	1	2	1	0	0	3	6	5	121
.049	2	54	0	0	0	6	1	61	2	2	0	2	6	0	2	0	1	0	0	2	0	6	147
.051	0	68	0	0	0	7	1	51	1	0	1	1	2	0	0	0	3	0	0	1	0	2	138
.053	1	18	0	0	0	2	0	6	1	0	0	3	2	0	2	0	2	1	0	1	1	0	40
.055	0	7	0	0	0	1	1	7	4	0	0	2	0	0	0	0	2	0	0	2	0	0	26
.057	2	13	0	0	0	2	0	37	6	0	0	2	0	0	0	0	4	1	0	0	1	0	68
.059	21	78	11	0	0	0	0	99	2	0	2	4	0	0	0	0	1	0	1	4	0	1	224
.061	8	6	16	0	0	1	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	4	76
.063	8	0	32	0	0	0	0	109	1	0	0	4	0	0	0	0	0	0	0	1	2	3	160
.065	11	47	70	0	1	0	2	614	0	0	0	1	0	0	0	0	1	0	0	5	3	2	757
.067	2	35	57	0	3	0	1	366	1	0	0	2	0	3	19	0	45	0	0	13	0	3	550
.069	5	18	50	0	1	0	2	227	0	2	0	2	1	0	2	0	15	1	0	13	0	4	343
.071	9	18	52	0	4	2	0	71	2	0	0	1	7	0	0	0	4	0	1	5	2	5	183
.075	19	126	74	1	8	0	2	294	3	0	0	1	0	2	0	0	20	0	0	10	7	14	582
.077	13	26	13	0	0	0	0	110	3	0	0	2	2	2	1	0	2	0	1	6	11	8	200
.079	17	48	14	0	0	0	0	129	3	2	0	1	6	2	42	0	3	0	0	7	2	26	302
.081	29	75	46	0	1	0	0	389	4	1	0	0	0	2	31	1	68	0	0	4	0	85	736
.084	14	11	45	0	0	0	0	207	7	0	0	2	0	0	9	0	7	0	0	0	1	8	311
.087	13	16	12	0	0	0	0	64	8	0	0	0	0	0	1	0	0	0	0	1	0	2	117

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae–Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
12.090	4	16	1	0	0	0	0	18	5	0	0	0	0	0	0	0	0	0	0	2	0	0	46
.092	0	50	3	0	0	0	0	71	9	0	0	0	0	0	0	0	0	0	0	1	1	16	151
.094	3	133	1	0	0	0	3	377	38	0	0	2	0	0	0	0	0	0	5	0	0	0	562
.097	3	61	4	0	0	0	0	101	16	1	0	0	0	0	0	0	0	0	0	2	0	19	207
12.100	12	14	11	0	0	0	3	56	5	1	0	1	0	0	1	0	0	0	0	6	1	11	122
.103	0	37	23	0	0	0	0	124	3	0	0	0	0	0	0	0	0	0	0	0	1	4	192
.106	26	41	33	0	0	1	0	319	5	0	0	0	0	1	4	0	6	0	0	6	3	7	452
.109	1	23	14	0	0	0	0	65	14	0	0	0	0	0	0	0	18	0	0	3	0	3	141
.112	6	5	17	0	0	0	0	32	1	0	0	0	0	0	0	0	0	0	0	1	1	4	67
.115	17	12	55	0	0	0	0	72	8	0	0	4	0	0	36	2	10	0	0	8	1	10	235
.118	0	159	9	0	0	0	0	107	6	1	0	0	0	2	11	7	18	1	0	7	0	2	330
.120	0	6	57	0	0	0	0	15	3	0	0	2	0	0	3	1	1	0	0	0	0	4	92
.122	0	5	36	0	2	0	0	30	2	0	0	0	0	0	0	0	0	0	0	0	4	3	82
.124	0	8	24	0	0	0	0	27	0	0	0	1	2	0	0	0	0	0	0	1	0	3	66
.126	0	22	17	0	14	0	0	108	0	0	0	1	0	2	0	0	0	0	0	1	1	6	172
.128	0	8	8	0	1	0	0	49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66
.130	0	0	3	0	2	0	0	12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	18
.132	0	7	8	0	0	0	0	8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	24
.134	0	28	11	0	0	0	1	20	1	0	0	0	0	0	0	0	0	0	0	0	0	1	62
.136	0	16	17	0	0	0	0	19	1	0	0	0	0	0	0	0	0	0	0	0	1	2	56
.138	0	12	6	0	0	0	0	10	3	0	1	0	2	0	0	0	0	0	0	0	0	2	36
.140	0	21	9	0	0	0	1	69	0	0	0	2	0	11	2	0	0	0	0	3	2	0	120
.142	0	110	11	0	1	0	1	84	11	3	2	4	3	1	3	0	0	0	0	0	1	4	241
.144	1	162	37	0	1	0	0	72	7	1	2	0	0	1	0	1	0	0	0	1	3	3	292
.146	0	13	1	0	1	1	0	11	1	1	0	0	0	0	0	0	0	0	0	1	0	0	30
.148	0	6	6	0	0	1	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	2	26
.150	0	36	0	1	0	0	2	86	1	0	0	0	0	0	17	3	0	0	0	1	4	0	151
.152	0	16	3	0	0	2	0	37	0	0	0	0	1	0	0	1	0	0	0	2	0	7	69
.154	0	11	0	0	0	0	0	12	0	1	0	0	4	0	0	0	0	0	0	0	1	2	31
.156	0	8	0	0	0	0	1	14	1	0	0	0	0	0	0	0	0	0	0	3	0	0	27
.158	0	50	1	0	0	0	0	41	4	1	0	1	0	0	0	1	0	0	0	1	0	0	100
.160	0	19	0	0	0	0	1	19	0	0	0	0	0	1	0	0	0	0	0	0	0	2	42
.162	0	1	0	0	0	0	0	5	0	0	1	0	0	0	0	0	0	0	0	1	0	0	8
.164	0	42	0	0	0	0	1	36	1	0	1	3	0	0	0	0	0	0	0	1	0	0	85
.184	0	49	25	0	0	1	0	45	4	5	0	1	0	0	0	0	0	0	0	1	1	1	133
.186	0	2	20	0	7	0	1	5	1	0	0	0	0	0	0	0	0	0	0	1	0	0	37
.188	0	4	31	0	2	0	1	8	3	0	0	1	2	0	0	1	0	0	0	0	0	3	56
.190	0	11	0	0	0	0	1	6	0	0	0	0	0	0	2	0	0	0	0	0	1	1	22
.192	0	27	7	0	0	0	0	45	3	1	0	1	0	1	0	0	0	0	0	0	2	1	88
.194	0	5	3	0	0	0	0	16	0	1	0	0	2	0	0	0	0	0	0	0	1	2	30
.196	0	5	34	0	10	0	0	22	0	0	0	5	0	0	0	0	3	0	0	3	8	7	97
.198	0	2	44	0	1	0	0	12	0	0	0	5	0	0	0	0	1	0	0	1	0	2	68
12.200	0	6	8	0	0	0	0	36	1	0	0	0	0	1	14	0	5	0	0	1	3	4	79
.203	1	4	38	0	0	0	0	91	2	0	0	0	0	0	1	0	0	0	0	0	0	3	140
.206	4	15	14	0	0	0	1	36	2	0	0	3	0	0	1	0	0	1	0	4	0	2	83
.209	4	6	35	0	0	0	0	70	4	0	0	1	0	0	2	0	0	0	0	6	0	1	129
.212	16	34	21	0	0	0	0	300	8	0	0	1	0	0	5	0	0	0	0	3	6	8	402
.215	7	45	23	0	0	0	0	202	6	0	3	0	0	0	12	0	0	0	0	7	0	3	308
.218	1	22	23	0	0	0	0	127	8	1	0	1	0	0	6	0	1	1	0	12	1	8	212
.221	2	44	13	0	0	0	0	209	24	2	0	2	0	0	0	0	1	0	4	8	4	17	330
.224	0	251	11	0	0	0	3	1089	66	5	0	2	0	0	2	0	1	0	10	13	0	10	1463
.227	1	94	14	0	0	0	3	162	27	0	0	1	1	1	1	0	0	0	1	3	5	22	336
.230	3	5	3	0	0	0	0	49	5	1	0	1	0	0	0	0	0	0	0	8	0	3	78
.233	45	52	24	0	0	0	2	250	10	1	0	2	0	0	0	0	0	0	0	3	0	1	390

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
12.235	25	59	11	0	3	0	4	280	11	0	1	1	0	0	11	0	6	0	0	2	0	5	419
.238	17	39	56	0	4	1	3	225	2	3	0	5	4	0	18	0	10	0	0	0	4	5	396
.240	11	19	70	0	3	0	7	54	2	0	0	1	5	0	24	0	10	0	0	6	1	10	223
.242	1	1	44	0	0	1	2	25	1	0	1	2	4	2	12	0	4	2	0	6	3	5	116
.244	3	14	99	1	3	2	2	105	3	2	0	1	8	1	10	0	14	1	0	29	3	2	303
.246	11	3	42	1	0	0	0	248	3	0	1	4	0	1	8	2	5	0	0	14	2	3	348
.248	1	6	8	0	1	0	1	51	0	0	0	1	1	0	1	0	1	0	0	4	0	2	78
.250	1	8	9	0	0	0	0	54	1	0	0	5	6	0	0	0	1	0	0	1	0	3	89
.252	1	3	5	0	0	1	0	44	2	0	0	1	1	0	0	0	0	0	0	0	0	6	64
.254	1	5	13	0	0	2	0	84	5	0	0	0	1	0	0	0	0	0	0	1	0	1	113
.256	3	1	15	0	0	0	2	23	5	0	0	0	5	0	0	0	0	0	0	1	0	1	56
.258	0	0	26	0	0	0	0	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	69
.260	2	20	4	0	0	1	0	74	4	2	0	4	0	0	0	1	1	0	0	4	0	3	120
.262	2	102	0	0	0	7	3	161	10	4	0	0	3	0	0	1	0	0	0	2	0	0	295
.264	2	20	0	0	0	29	1	26	10	0	0	3	8	0	0	0	0	0	0	3	2	6	110
.265	3	18	0	0	0	32	1	54	5	7	0	2	17	0	0	0	2	0	0	1	2	1	145
.268	0	105	0	0	0	14	1	156	6	6	0	0	4	0	0	0	5	0	0	12	1	6	316
.270	1	29	0	0	0	17	1	60	6	4	0	2	7	0	0	0	0	0	0	3	1	3	135
.272	4	43	0	0	0	6	2	81	4	1	0	5	11	0	0	1	0	0	0	3	5	2	168
.274	0	40	0	0	0	36	1	85	5	1	0	8	4	0	0	0	1	0	0	1	1	4	187
.276	0	138	0	0	0	6	0	20	0	0	0	0	1	0	0	1	0	0	0	0	0	1	167
.278	1	165	0	0	0	1	2	45	0	0	0	1	3	0	0	0	0	0	0	0	1	0	219
.280	0	22	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	0	0	1	29
.282	1	23	0	0	0	0	0	8	0	0	0	1	1	0	0	0	0	0	0	0	1	0	35
.284	0	120	0	0	0	0	2	16	0	0	0	0	0	0	0	0	0	0	0	0	0	1	139
13.001	8	93	108	0	1	8	0	41	0	1	0	6	0	0	1	0	0	0	0	0	1	6	274
.003	14	1165	39	0	2	10	1	385	14	1	0	9	0	0	0	0	2	0	0	11	0	4	1657
.005	54	310	18	0	0	11	3	1075	0	1	0	14	0	0	3	0	1	0	0	7	0	6	1503
.007	9	13	38	0	2	4	3	133	0	0	0	10	0	0	7	0	2	0	0	4	0	0	225
.009	9	10	15	0	1	0	1	494	0	0	0	7	0	0	7	0	0	0	0	1	0	5	550
.011	6	2	15	0	0	1	1	374	0	0	0	0	0	0	0	0	0	0	0	2	0	0	401
.013	18	9	5	0	0	0	0	207	0	0	0	1	1	1	1	0	0	0	0	5	0	3	251
.015	4	1	21	0	0	0	0	479	0	0	0	2	0	0	4	0	0	0	0	2	0	0	513
.017	16	63	20	0	1	0	2	559	0	0	0	3	0	5	8	0	0	0	0	3	5	3	688
.019	9	82	19	0	0	2	0	1219	0	0	9	5	62	10	106	0	2	0	0	275	48	12	1860
.021	4	2	0	0	0	0	0	409	0	0	1	1	176	0	24	0	0	0	0	58	6	9	690
.022	1	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	5
.028	4	6	0	0	0	0	0	2	0	0	1	0	1	0	1	0	0	1	0	0	0	0	16
.030	7	0	0	0	0	0	0	24	0	0	0	7	2	0	7	0	0	0	0	9	0	0	56
.032	0	24	0	0	0	0	0	44	4	0	0	4	8	0	52	0	4	0	0	36	12	0	188
.034	23	61	4	0	0	0	2	158	0	0	0	4	0	6	43	0	7	1	1	46	8	3	367
.036	8	0	2	0	0	0	0	13	0	0	1	3	0	2	0	0	1	0	0	1	0	0	31
.038	28	0	20	0	0	0	0	142	0	0	0	8	0	0	2	0	0	0	0	2	0	10	212
.040	20	17	65	0	0	0	4	469	0	1	2	2	1	0	20	0	0	0	0	10	0	10	621
.042	11	14	85	0	1	0	0	307	0	0	0	3	0	1	4	0	4	0	0	15	0	3	448
.044	10	14	73	0	0	3	1	109	0	1	0	3	0	0	2	0	1	0	1	1	0	1	220
.046	10	78	95	0	1	5	10	105	11	0	0	6	1	0	1	0	3	0	0	3	2	16	347
.048	29	311	177	0	3	6	5	300	22	0	2	12	1	1	1	3	44	0	0	6	0	15	948
.050	10	41	68	0	0	8	1	133	2	0	0	5	0	0	0	0	5	0	0	1	0	3	277
.052	13	199	73	0	0	3	1	79	24	0	0	6	1	0	0	0	4	0	0	22	4	26	455
.054	14	91	26	0	0	1	4	77	24	0	0	2	2	3	11	17	5	0	1	9	7	8	302
.056	33	513	10	0	0	0	18	144	28	0	0	2	1	0	0	2	7	0	0	15	9	4	786
.058	6	338	9	0	0	0	2	83	10	0	0	3	0	0	7	0	3	0	0	0	3	6	470

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
.060	5	26	0	0	0	0	0	59	4	0	0	1	0	0	18	0	0	0	0	2	3	2	120
.062	7	8	1	0	0	0	0	44	5	0	1	0	0	0	1	0	0	0	0	8	5	3	83
.064	15	71	6	0	0	0	2	274	21	0	1	2	0	0	1	0	0	0	1	0	5	7	406
.065	2	72	6	0	0	0	4	31	6	0	0	1	0	0	0	0	0	0	0	1	4	1	128
.067	7	54	3	0	0	0	1	34	6	0	0	1	0	0	0	0	0	0	0	1	0	0	107
.069	37	60	33	0	0	1	6	99	7	0	0	7	0	0	1	0	0	0	0	3	0	3	257
.071	37	572	8	0	1	8	6	318	9	0	0	8	0	1	14	6	3	0	1	13	7	3	1015
.073	42	167	53	0	2	27	1	172	27	0	0	11	0	0	3	7	10	1	1	16	7	8	555
.075	8	21	3	0	1	0	0	39	25	0	0	6	0	0	1	2	1	1	0	1	0	4	113
.077	0	59	38	0	0	0	2	89	14	2	0	1	0	0	5	3	3	0	1	2	2	36	257
.079	0	135	43	0	0	0	0	69	3	3	2	1	0	0	5	0	6	0	0	1	0	0	268
.081	2	164	13	0	0	0	1	16	2	0	1	0	0	0	0	8	4	0	0	1	0	3	215
.083	5	43	4	0	0	0	0	17	1	0	0	6	0	0	0	1	0	0	0	0	0	1	78
.085	0	2	1	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
.087	0	66	6	0	0	1	0	37	0	1	0	0	1	0	0	0	0	0	0	3	0	0	115
.089	0	26	29	0	0	0	0	105	2	0	0	1	0	0	0	0	0	0	2	3	0	15	183
.091	0	11	2	0	0	1	1	49	6	0	0	3	2	0	2	0	0	1	1	3	2	17	101
.093	0	3	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	2	13
.095	6	146	4	1	0	29	3	195	1	0	2	4	7	0	10	7	0	0	6	12	2	4	439
.097	3	103	11	0	0	7	2	205	2	2	0	6	4	0	1	5	0	1	4	9	2	1	368
.099	0	16	7	0	1	0	1	48	0	0	0	1	1	0	0	0	0	0	6	1	1	0	83
13.101	3	11	0	0	1	0	0	45	2	3	0	1	7	0	0	7	0	0	0	4	1	0	85
.103	1	162	6	0	1	3	4	255	5	0	0	5	3	0	0	7	0	0	3	14	3	7	479
.105	0	50	4	0	0	1	1	166	2	0	0	3	1	0	0	2	0	1	4	5	2	0	242
.107	0	1	0	0	0	0	0	13	0	0	0	0	0	0	0	1	0	0	1	0	0	0	16
.109	0	12	0	0	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	2	0	0	41
.111	0	18	1	0	0	0	0	49	1	0	0	1	0	0	0	0	0	0	0	1	0	0	71
.113	0	30	2	0	0	0	1	72	2	0	0	0	2	1	0	0	0	0	0	2	0	0	112
.115	0	8	0	0	0	0	0	25	1	0	0	0	1	0	0	0	0	0	0	1	0	1	37
.117	0	9	4	0	0	0	4	52	1	2	0	1	3	1	0	0	0	0	0	1	1	2	81
.119	0	36	0	0	0	0	4	86	4	0	0	0	0	0	0	4	0	0	0	0	0	0	134
.121	0	17	3	0	0	0	0	22	1	0	0	0	0	0	0	0	0	0	0	0	0	2	45
.123	0	3	2	0	0	0	0	3	1	1	0	2	0	0	0	0	0	0	2	0	0	0	14
.125	0	1	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	5
.127	0	20	2	0	0	0	3	39	1	1	0	1	1	0	0	0	0	0	0	0	0	1	69
.129	0	11	1	0	0	0	2	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28
.131	0	6	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	3	16
.133	0	5	4	0	0	0	0	9	0	0	1	0	0	0	0	0	0	0	0	0	2	0	21
.135	0	56	1	0	0	0	1	78	2	0	0	1	1	0	0	0	0	0	0	0	0	0	140
.137	0	40	1	0	0	0	0	50	1	0	0	0	0	0	0	2	0	0	0	2	0	0	96
.139	0	12	1	0	0	0	0	8	0	0	0	0	0	0	0	1	0	0	0	0	1	1	24
.141	0	4	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
.143	0	76	2	0	0	0	0	86	1	0	0	1	1	0	0	0	0	0	0	0	6	0	173
.145	0	20	2	0	0	0	2	44	2	0	0	0	2	0	0	0	0	0	0	0	0	0	72
.147	0	17	0	0	0	0	0	33	0	0	0	3	4	0	0	2	0	0	0	3	3	0	65
.149	0	14	6	0	0	0	0	29	0	0	0	2	0	0	0	0	1	0	0	0	0	3	59
.151	0	22	0	0	3	0	1	72	0	1	0	0	0	2	0	0	0	0	0	0	1	1	103
.153	0	103	1	0	1	3	1	394	2	1	1	5	3	0	0	1	0	2	0	17	1	3	539
.155	0	8	4	0	0	0	0	16	0	2	0	2	0	0	0	0	0	0	0	2	4	0	38
.157	0	8	8	0	0	1	0	45	1	0	0	0	1	0	1	0	0	0	0	0	0	2	67
.159	0	12	5	0	0	8	0	53	1	1	0	1	0	0	4	2	0	0	0	2	2	1	92
.161	0	24	6	0	0	0	0	65	3	0	0	0	2	0	0	0	0	0	0	0	0	2	102
.163	0	5	2	0	0	0	0	14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	22
.165	0	4	17	0	0	0	0	24	0	0	0	1	2	0	0	0	0	0	0	0	0	0	48

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
13.167	0	19	11	0	0	0	0	33	0	0	0	0	0	0	0	1	0	0	0	1	0	1	66
.169	0	83	10	0	0	0	0	169	0	0	0	1	0	0	0	0	0	0	0	0	0	1	264
.171	0	18	38	0	0	0	1	104	10	0	0	3	0	0	14	1	0	0	0	2	1	3	195
.173	7	4	10	0	0	3	1	121	2	1	0	3	0	0	6	1	0	0	0	1	0	4	164
.175	22	176	14	0	3	1	0	245	5	0	0	5	0	3	45	1	2	0	0	6	5	2	535
.179	15	111	75	0	0	0	0	133	2	1	0	1	0	1	7	3	4	0	0	2	0	0	355
.183	50	39	39	0	2	3	0	80	13	0	0	15	0	0	7	0	22	1	0	3	2	1	277
.187	43	29	49	0	0	0	3	67	7	0	0	3	0	0	1	2	21	0	1	6	0	4	236
.191	10	148	23	0	0	0	1	126	24	0	0	5	0	1	7	1	18	0	0	8	1	3	376
.195	10	202	2	0	0	0	0	182	2	0	0	0	0	0	0	0	0	1	0	1	0	3	403
.199	5	28	3	0	0	0	0	55	5	0	0	2	0	0	0	0	0	0	1	1	0	2	102
13.203	3	16	2	0	0	0	0	20	2	0	0	0	0	0	0	0	0	0	1	3	0	3	50
.207	11	161	4	0	0	0	0	129	11	0	0	1	0	0	0	0	0	0	0	2	0	1	320
.211	5	36	2	0	0	0	1	68	3	0	0	0	0	0	1	0	0	0	0	0	1	1	118
.215	6	7	5	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	2	27
.219	9	10	14	0	0	0	0	11	0	0	1	0	0	0	0	0	0	0	0	0	0	4	49
.223	2	20	3	0	0	0	0	32	5	0	0	2	0	0	0	0	3	0	0	1	3	1	72
.227	9	38	30	0	0	0	0	121	12	0	1	1	0	4	1	0	3	0	0	0	1	0	221
.231	9	34	35	0	0	0	0	82	0	0	0	1	0	0	0	0	2	0	1	1	0	1	166
.235	9	36	78	0	0	1	1	106	0	2	0	1	0	1	1	1	5	0	0	3	6	7	258
.237	6	47	97	0	1	0	1	189	2	1	0	3	0	0	7	0	7	0	0	3	4	3	371
.239	3	44	58	0	0	0	3	179	0	0	0	1	0	0	0	0	7	0	0	4	0	2	301
.241	2	5	36	0	0	0	0	59	1	0	0	0	0	0	1	0	6	0	0	0	0	4	114
.243	11	13	5	0	0	0	0	93	0	0	0	3	1	0	0	0	5	0	0	1	0	9	141
.245	7	14	11	0	1	0	0	57	3	3	0	2	0	0	0	1	0	0	0	15	0	0	114
.247	9	11	3	0	0	0	0	26	0	2	0	1	0	0	1	0	0	0	0	7	0	0	60
.249	1	3	4	0	0	0	0	46	0	0	0	0	0	0	0	0	0	0	0	1	0	0	55
.251	6	10	9	0	0	1	2	25	15	2	3	1	0	0	3	0	1	1	0	1	0	1	81
.253	20	22	2	0	0	2	4	6	2	0	2	2	0	0	0	0	6	0	0	80	0	0	148
.255	7	29	0	0	0	2	0	29	2	2	0	3	4	1	15	0	0	0	0	29	3	2	128
.257	8	3	0	0	0	0	2	10	3	0	0	1	5	0	0	0	0	0	0	2	0	4	38
.259	17	18	0	0	0	4	0	23	0	0	0	1	2	0	5	0	0	0	0	3	0	6	79
.261	8	37	0	0	0	3	0	13	6	3	0	1	5	0	0	0	1	0	0	44	0	1	122
.263	19	54	0	0	0	4	0	46	1	5	0	3	3	1	11	0	0	0	0	15	1	2	165
.265	6	13	0	0	0	0	8	14	6	1	1	0	5	0	2	0	2	0	0	5	5	1	69
.266	0	2	0	0	0	0	0	14	0	0	0	0	22	0	2	0	0	0	0	8	5	1	54
.268	3	26	0	0	0	7	0	33	5	1	0	1	3	0	1	0	3	0	0	2	4	7	96
.270	4	20	0	0	0	5	4	9	7	1	0	1	1	12	1	0	2	0	0	3	2	6	78
.272	2	3	1	0	0	0	2	13	1	0	0	1	1	0	0	0	1	0	0	1	0	2	28
.274	1	52	0	0	0	21	6	63	15	4	1	8	3	3	2	0	7	0	0	9	2	1	198
.276	5	91	0	0	0	13	3	89	10	0	0	1	3	3	20	0	2	0	0	9	1	0	250
.278	1	21	0	0	0	18	2	7	0	3	0	1	2	0	0	0	1	0	0	0	0	1	59
.280	8	8	0	0	0	27	2	31	2	15	0	0	34	0	0	1	0	0	0	6	0	0	134
.282	0	36	0	0	0	9	6	89	5	20	0	0	7	1	0	0	0	0	0	15	1	0	189
.284	18	61	0	0	0	23	3	34	10	15	0	1	13	2	0	0	0	0	0	3	0	2	185
13.318	13	1	0	0	0	5	0	3	0	2	0	2	5	0	1	0	0	0	0	5	0	0	37
.320	8	16	9	0	0	0	0	18	1	4	1	5	2	0	13	0	0	0	0	23	0	0	100
.322	0	5	0	0	0	0	0	0	0	0	1	0	0	2	9	0	0	0	0	6	0	0	23
.324	10	4	1	0	0	3	0	26	1	0	0	0	1	3	4	0	1	0	0	1	0	0	55
.326	13	10	1	0	0	0	0	44	0	4	0	0	2	0	18	0	0	0	0	4	0	0	96
.328	2	9	1	0	0	0	0	35	2	1	0	5	1	1	7	0	23	0	0	4	3	2	96
.330	4	12	8	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	4	0	0	52
.332	11	2	19	0	0	0	0	63	0	0	0	0	0	0	2	0	0	1	0	1	0	1	100

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
13.334	37	21	17	0	0	0	1	116	2	0	0	3	0	0	1	0	1	0	0	5	3	1	208
.338	9	49	26	0	0	0	0	295	0	0	1	0	0	2	5	0	8	0	0	24	0	3	422
.340	4	11	23	0	0	2	0	47	0	0	0	4	0	0	0	0	4	1	0	4	0	0	100
.342	9	24	21	0	0	2	0	76	4	0	1	3	0	0	4	0	0	0	0	1	0	2	147
14.001	39	97	1	1	1	0	6	867	4	5	2	0	194	0	9	1	12	0	0	261	15	195	1710
.006	32	19	38	0	0	0	1	66	2	0	8	0	2	0	10	0	0	0	0	15	25	8	226
.008	34	4	32	0	0	2	1	86	1	0	2	0	1	0	1	0	2	0	0	25	4	2	197
.010	14	19	40	0	0	4	2	198	1	0	2	3	0	0	0	1	0	0	0	12	2	3	301
.012	6	1	7	0	0	1	1	57	1	0	0	3	1	0	0	2	0	0	0	2	4	4	90
.014	42	4	9	0	0	1	0	67	0	0	1	0	9	0	2	0	0	0	0	30	5	28	198
.016	19	1	20	0	0	0	0	8	0	0	0	2	4	0	2	0	0	0	0	44	16	5	121
.017	17	2	16	0	0	1	0	61	1	0	0	2	0	0	0	0	0	0	0	4	0	1	105
.018	41	48	64	0	0	2	2	424	0	0	0	4	0	0	0	0	5	0	0	24	1	19	634
.020	6	10	12	0	0	0	1	229	1	0	0	2	0	0	0	0	0	0	0	10	0	54	325
.022	7	22	14	0	0	0	3	80	0	0	0	5	1	0	0	0	1	0	0	32	4	0	169
.024	6	0	0	0	0	0	0	47	0	0	1	0	0	1	0	0	0	0	0	29	5	22	111
.027	23	31	42	0	0	0	3	387	0	0	2	7	9	0	6	0	0	0	0	87	34	19	650
.029	24	42	25	0	0	0	5	382	0	1	1	2	6	0	1	3	1	0	0	119	47	26	685
.031	30	43	46	0	0	9	2	594	15	0	2	6	0	0	1	1	3	0	0	75	5	43	875
.033	21	5	0	0	0	0	2	26	1	0	0	1	0	0	0	0	0	0	0	9	3	3	71
.040	48	2	0	0	0	0	2	36	8	0	3	4	0	0	6	0	0	0	1	21	3	21	155
.043	65	17	2	0	0	0	1	159	8	0	0	8	1	0	22	0	1	0	3	15	7	4	313
.047	111	3	4	0	0	0	4	22	3	0	0	2	0	3	9	0	6	0	0	7	0	44	218
.051	225	27	1	1	0	0	5	78	3	0	0	1	0	1	46	0	11	0	1	1	3	25	429
.055	154	2	2	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	4	0	8	210
.060	139	0	0	0	0	0	0	18	0	0	1	2	0	0	0	0	0	0	0	54	2	15	231
.066	13	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11	0	1	26
.069	20	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	97	0	0	119
.076	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11	0	0	15
.078	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.081	2	16	1	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37
.084	2	3	0	0	0	0	0	4	0	0	0	0	0	1	0	0	0	0	0	1	0	2	13
.086	2	0	0	0	1	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	3	13
.088	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
.091	2	40	0	0	0	0	1	43	0	0	0	0	0	0	0	0	0	0	0	3	2	0	91
.095	2	3	0	0	0	0	1	50	0	0	0	0	0	0	0	1	0	0	1	1	0	0	59
.099	2	3	0	0	0	1	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21
14.103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	11	0	14
.110	0	8	0	0	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	1	0	1	37
.112	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	5
.114	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.115	2	6	0	0	1	0	0	5	0	0	0	1	0	0	0	0	0	0	0	2	0	0	17
.117	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5
.118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.120	1	6	0	0	1	0	0	15	0	0	0	0	0	1	1	0	0	0	0	0	0	0	25
.122	2	11	1	0	0	1	0	19	0	0	0	0	0	0	0	1	0	0	0	1	0	0	36
.123	7	23	0	0	0	7	0	51	0	0	0	1	1	0	0	1	0	0	2	9	0	0	102
.124	7	76	0	0	0	[illegible]	0	152	0	0	0	0	4	2	0	3	0	0	2	12	0	4	268
.126	3	20	1	0	2	6	0	53	0	1	0	0	3	0	0	2	0	0	3	4	1	15	114
.127	5	5	0	0	0	0	1	22	0	0	0	0	2	0	0	3	0	0	0	3	0	3	44
.128	5	60	0	0	3	9	0	145	0	0	0	0	5	0	0	6	1	0	1	13	0	0	248
.130	3	44	1	0	1	7	0	45	0	0	0	2	2	0	4	3	2	1	5	3	4	15	142

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagidae	Gonostomatidae	Sternoptychidae	Astronesthidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Myctophidae	Paralepididae	Scopelarchidae	Eel leptocephali	Melamphaeidae	Bregmacerotidae	Exocoetidae	Scombridae	Gempylidae-Trichiuridae	Nomeidae	Bramidae	Chiasmodontidae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
14.131	0	14	0	0	0	0	1	2	0	2	0	0	0	0	0	1	0	0	0	0	2	2	24
.132	8	17	3	0	0	0	0	8	1	2	2	3	0	0	0	0	2	2	0	5	1	0	54
.134	0	4	2	0	0	0	0	11	0	0	2	2	0	0	0	2	2	0	0	1	0	1	27
.136	1	18	3	0	0	0	0	43	0	0	0	0	0	0	0	0	0	0	1	0	0	0	66
.138	9	92	32	0	0	0	0	29	1	1	0	0	0	1	9	3	5	0	1	1	1	4	189
.142	1	53	31	0	0	0	4	110	0	0	0	1	0	0	1	2	5	0	0	1	0	4	213
.146	46	111	9	0	2	0	2	176	10	0	0	3	0	1	8	2	17	1	0	2	0	4	394
.150	34	48	13	0	0	0	1	52	4	0	0	4	0	4	5	1	2	1	3	6	0	87	265
.154	34	382	17	0	0	0	0	92	6	0	0	5	0	2	7	0	1	0	1	20	1	2	570
.158	0	224	2	0	0	0	1	30	10	0	0	0	0	0	3	0	6	0	0	27	5	21	329
.164	8	53	0	0	0	0	2	135	39	0	3	0	0	0	6	1	0	0	1	8	2	26	284
.172	1	97	20	0	0	0	0	26	0	0	2	0	0	0	16	0	0	0	0	43	3	1	209
.174	3	37	12	0	0	0	0	26	7	0	0	1	0	0	0	0	0	0	0	12	7	32	137
.177	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	77	5	0	86
.183	1	1	0	0	1	0	0	4	1	0	0	0	0	0	0	0	0	0	0	1	0	2	11
.188	34	168	5	0	0	4	1	261	25	1	5	7	0	3	36	1	3	0	0	5	2	0	561
.194	161	129	1	0	0	3	4	1753	40	0	4	23	0	0	22	2	12	0	0	12	7	24	2197
.195	54	17	0	0	0	2	1	252	24	3	0	1	0	0	0	1	0	0	0	6	0	68	429
.199	15	203	20	0	1	2	0	16	13	3	3	5	0	0	20	0	2	1	1	12	5	4	326
14.203	3	2	12	0	0	0	0	179	2	0	0	1	0	0	1	0	2	0	0	4	0	2	208
.209	5	2	5	0	0	0	0	25	0	0	2	0	1	10	0	0	2	0	0	3	0	1	56
.213	34	96	9	0	1	2	2	206	1	2	1	3	0	1	11	0	2	0	0	6	1	0	378
.218	27	39	1	0	0	1	0	177	0	2	0	1	0	2	4	0	1	0	0	3	1	7	266
.220	2	3	6	0	0	0	0	22	9	0	0	1	0	0	13	0	0	0	0	5	4	21	86
.222	2	5	2	0	1	2	2	49	0	2	1	1	0	0	1	1	0	0	0	1	2	1	73
.224	12	37	19	0	0	0	2	115	2	1	1	1	0	0	8	1	0	0	0	12	4	6	221
.228	2	5	10	0	0	1	0	30	3	2	1	2	1	0	2	0	0	0	0	14	3	0	76
.230	1	5	9	0	1	0	1	41	2	0	0	1	0	0	10	0	0	1	0	8	2	8	90
.232	9	49	23	0	0	0	0	31	1	2	0	3	0	0	12	0	0	0	0	8	0	1	139
.234	9	869	1	0	0	3	8	228	10	0	12	1	0	0	185	9	9	0	0	5	1	350	1748
.236	3	16	3	0	0	1	0	34	2	1	1	3	0	0	10	0	0	0	0	8	1	0	83
.240	21	36	18	0	0	2	0	116	16	2	2	5	1	0	85	1	2	0	0	12	3	8	330
.243	24	28	11	0	0	0	0	44	7	0	1	1	0	1	5	0	1	0	0	3	0	2	128
.247	4	52	9	0	0	2	0	86	9	0	0	0	0	0	1	0	1	0	0	2	2	1	169
.251	11	25	6	0	1	1	0	25	8	0	0	4	0	0	1	0	0	0	0	8	0	1	91
.255	210	86	11	0	1	2	0	227	0	1	0	1	0	0	59	0	2	1	0	8	5	17	631
.259	16	40	6	0	0	4	1	53	0	3	1	6	0	0	0	3	0	2	0	7	3	4	149
.263	2	233	4	0	0	0	0	105	0	0	0	1	0	0	0	0	4	0	0	3	0	2	354
.267	3	33	3	0	0	0	1	8	0	0	0	2	0	0	0	0	0	0	0	6	1	0	57
.276	9	58	0	0	0	1	0	13	0	2	0	3	0	0	0	0	3	0	0	3	3	0	95
.280	7	63	0	0	0	4	2	44	1	0	0	0	0	0	0	6	4	0	0	9	4	10	154
.283	3	13	0	0	2	0	0	22	0	1	0	4	0	0	0	1	0	0	1	2	0	1	50
.287	5	62	12	0	1	0	0	15	0	1	0	2	0	0	0	3	10	1	0	10	0	1	123
.291	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.295	4	1	2	0	0	0	0	65	0	0	0	1	0	0	63	1	1	0	0	8	3	1	150
14.300	287	0	5	0	0	0	2	18	0	0	0	0	0	0	1	0	0	0	0	1	0	8	322
.303	493	10	6	0	0	0	3	200	0	0	0	2	0	0	0	0	0	0	0	9	0	0	723
.306	34	2	1	0	0	0	2	32	8	0	0	6	0	0	0	0	0	0	1	1	0	5	92
.310	91	21	18	0	0	0	3	96	6	0	0	8	0	0	0	0	0	0	0	0	0	5	248
.314	24	25	20	0	0	0	2	59	7	0	0	4	0	0	0	0	0	0	0	2	0	1	144
.318	32	70	39	0	0	9	1	566	0	0	0	4	0	0	1	3	0	0	1	93	0	9	828
.323	11	24	37	0	0	0	3	165	0	0	0	2	0	0	0	0	0	0	0	15	0	5	262
.326	27	66	31	0	0	4	4	659	0	0	2	13	1	0	8	1	0	0	0	49	13	33	911
.330	0	1	3	0	0	0	0	23	1	0	0	0	5	0	0	1	0	0	0	1	0	3	38

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I.

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
11.022	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	4
.025	0	1	1	1	0	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	11
.027	0	1	1	4	0	0	0	4	0	0	2	0	0	1	0	0	0	0	0	0	1	0	14
.030	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.032	0	0	0	6	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
.034	0	0	2	10	0	0	0	16	0	0	7	0	0	0	0	0	0	0	0	0	0	0	35
.036	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
.038	0	0	2	10	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	2	2	21
.040	0	0	5	4	0	0	0	39	0	0	1	0	0	0	0	0	0	0	4	0	2	0	55
.044	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
.046	0	0	4	41	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	50
.048	0	0	1	6	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	20
.050	0	0	0	33	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	36
.052	0	0	0	56	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	58
.054	0	0	3	147	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	159
.056	0	0	0	56	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	3	67
.058	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	28
.060	0	0	4	53	0	0	1	0	3	0	9	0	0	0	0	0	0	0	1	0	1	0	72
.062	0	0	0	16	0	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0	1	0	21
.064	0	0	2	43	0	0	0	0	0	0	2	0	0	0	0	3	0	0	0	0	1	0	51
.066	0	0	4	14	0	0	2	0	9	0	4	0	0	0	20	3	0	0	4	1	2	0	63
.068	0	0	67	33	1	0	0	0	14	2	4	7	0	4	21	32	1	0	21	8	0	14	229
.070	0	1	15	8	0	0	0	0	6	0	0	0	0	1	48	6	2	0	4	0	0	5	96
.072	0	0	28	6	0	0	0	0	22	1	12	7	0	0	44	21	2	0	24	7	0	4	178
.076	0	0	0	23	0	0	0	0	0	0	27	0	0	0	0	20	5	0	0	1	1	13	90
.080	0	0	1	18	0	0	0	2	1	0	6	0	0	0	3	2	0	0	1	0	1	1	36
.084	0	0	0	63	0	0	0	0	7	0	13	0	0	0	1	3	0	0	2	0	0	42	131
.088	0	0	2	10	0	0	0	1	9	0	67	0	0	1	7	0	2	0	0	2	0	3	104
.094	0	0	5	8	0	0	0	0	4	0	32	0	0	0	9	1	0	0	0	1	4	2	66
.098	0	0	3	107	0	0	2	50	109	1	404	0	12	1	180	8	10	0	9	1	1	9	907
11.102	0	0	0	21	0	0	0	3	26	0	12	0	0	0	26	0	0	0	1	0	0	10	99
.106	0	0	0	6	0	0	0	0	4	0	0	0	0	0	7	0	0	0	4	0	0	1	22
.110	0	0	0	41	0	0	0	1	1	0	3	0	0	0	7	1	0	0	1	1	0	1	57
.114	0	0	0	182	0	0	0	3	9	0	31	0	0	1	11	1	1	0	2	0	2	0	243
.118	0	0	0	70	0	0	0	1	1	0	9	0	0	0	0	0	0	0	0	0	0	3	84
.120	0	0	0	8	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	9
.124	0	0	0	37	0	0	0	2	5	0	17	0	0	1	0	3	0	0	0	0	0	1	66
.128	0	1	0	31	0	0	0	3	1	0	29	0	0	2	0	6	0	0	16	1	0	8	98
.130	0	1	11	0	0	0	0	0	3	0	4	0	0	0	1	0	0	0	0	0	8	1	29
.132	0	4	3	0	0	0	0	0	1	3	0	0	0	0	1	0	0	0	4	0	0	0	16
.134	0	26	39	0	0	0	0	0	0	0	30	0	0	0	0	2	0	0	0	0	6	6	109
.136	0	30	39	0	0	0	0	0	5	4	5	0	0	0	8	2	0	0	60	0	15	0	168
.138	0	0	10	0	1*	0	0	0	1	2	1	0	0	0	1	0	0	0	2	1	0	2	21
.140	0	2	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	3	0	1	0	12
.142	0	4	6	0	0	0	0	0	1	0	16	0	0	0	0	0	0	0	31	0	2	9	69
.146	0	10	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	1	17
.148	0	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	3	13
.150	0	0	4	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	15	0	0	13	38
.152	0	10	13	0	0	0	0	3	19	1	20	0	0	0	1	0	3	0	43	0	2	0	115
.154	0	0	0	0	0	0	0	0	1	0	6	0	0	0	0	0	0	0	5	0	0	3	15

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
11.156	0	4	0	0	0	1	0	0	9	0	9	0	0	0	0	0	0	0	5	0	0	1	29
.158	0	8	14	0	0	2	0	0	23	0	7	0	0	0	2	0	0	0	27	0	1	19	103
.159	0	19	14	0	0	1	0	0	16	0	17	0	0	0	2	1	0	0	25	0	0	22	117
.161	0	3	0	0	0	0	0	0	2	0	2	0	0	0	1	0	0	0	0	0	0	2	10
.163	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.167	0	1	5	0	0	0	0	0	1	0	6	1	0	0	2	0	0	0	4	0	0	0	20
.169	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
.171	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
.173	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	5
.175	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	4
.177	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
.179	0	2	1	0	0	0	0	2	0	0	7	0	0	0	1	0	0	0	0	0	0	0	13
.181	0	3	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	3	13
.183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.185	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	4
.187	0	4	0	0	0	0	0	4	0	0	11	0	0	0	0	0	0	0	1	0	0	4	24
.189	0	3	5	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	5	19
.191	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	2
.195	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	4
.197	0	14	13	0	0	1	0	0	3	0	7	0	0	0	3	0	0	0	6	0	5	8	60
.199	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	2	0	0	3	9
11.201	0	1	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	1	0	0	2	8
.203	0	0	4	0	0	0	0	0	0	0	4	0	0	0	4	0	0	0	2	0	1	2	17
.205	0	5	9	0	0	0	0	0	6	0	3	0	0	0	5	0	0	0	8	0	0	4	40
.207	0	7	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	3	0	0	8	21
.209	0	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	4	0	0	2	12
.211	0	3	0	0	0	0	0	0	13	0	5	0	0	0	0	0	0	0	2	0	0	5	28
.213	0	17	16	0	0	0	0	0	6	0	5	0	0	0	3	0	0	0	17	0	4	3	71
.215	0	4	0	0	0	0	0	0	13	0	8	0	0	0	2	2	0	0	7	0	0	8	44
.217	0	1	2	0	0	0	0	0	5	0	2	0	0	0	0	0	0	0	5	0	0	1	16
.219	0	3	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	3	0	1	0	10
.221	0	0	26	0	0	0	0	0	11	0	4	3	0	0	1	8	0	0	19	0	0	2	74
.223	0	4	0	0	0	0	0	0	3	0	2	0	0	0	2	2	0	0	6	0	1	0	20
.226	0	2	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2	0	0	1	7
.228	0	0	2	0	0	0	0	0	4	0	0	0	0	0	0	6	1	0	3	0	0	0	16
.234	0	9	1	14	0	0	0	0	7	0	2	0	0	0	1	4	0	0	1	0	0	7	46
.238	0	0	0	3	0	0	0	0	1	0	2	0	0	0	0	0	0	0	2	0	0	2	10
.242	0	0	0	58	0	0	0	2	9	0	13	0	0	1	2	3	0	0	1	2	0	4	95
.246	0	0	1	62	0	0	0	1	14	0	98	0	0	0	16	0	0	0	0	0	0	6	198
.250	0	0	1	17	0	0	0	2	15	0	8	0	0	0	11	1	0	0	0	1	0	1	57
.254	0	1	2	18	0	0	2	1	30	0	4	0	0	0	85	0	0	0	4	0	0	2	149
.258	0	0	0	32	0	0	0	5	1	0	20	0	0	1	0	0	0	0	36	0	11	2	108
.262	0	0	4	57	0	0	0	2	2	0	5	0	0	4	4	2	0	0	0	0	0	5	85
.266	0	1	3	19	0	0	0	0	0	0	1	0	0	1	3	3	0	0	1	1	2	3	38
.270	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	1	2	2	17
.278	0	0	9	51	0	1	0	2	3	0	20	0	2	1	7	13	4	0	0	2	0	1	116
.282	0	0	0	14	0	0	0	0	7	0	19	4	0	0	26	3	0	0	8	1	0	0	82
.285	0	0	0	7	0	0	0	0	6	0	0	0	0	0	6	1	0	0	2	0	0	8	30
.287	0	0	17	2	0	0	0	0	14	1	6	2	0	0	16	18	0	0	5	1	2	3	87
.289	0	0	33	17	0	0	0	0	19	8	4	2	0	0	8	12	2	0	14	0	0	12	131

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
11.291	0	2	3	13	0	0	0	0	6	0	1	0	0	1	2	3	0	0	0	0	1	7	39
.293	0	0	0	36	0	0	0	0	2	0	2	0	0	1	1	1	0	1	3	0	2	1	50
.295	0	0	7	94	0	0	0	0	4	0	18	0	0	0	0	1	0	1	4	0	0	1	130
.297	0	0	6	263	0	0	0	0	3	0	3	0	0	0	0	0	0	0	1	0	1	20	297
.299	0	1	0	23	0	0	0	0	2	0	2	0	0	0	1	0	0	0	0	0	0	0	29
11.301	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	8
.303	0	0	0	42	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	44
.306	0	0	0	37	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	40
.308	0	0	0	6	0	0	0	0	0	0	2	0	0	0	0	0	0	0	5	0	0	0	13
.310	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	15
.312	0	0	0	16	0	0	0	1	0	0	1	0	0	0	0	0	0	0	4	0	0	4	26
.314	0	0	2	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	1	1	27
.316	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4	0	0	0	8
.318	0	0	0	26	0	0	1	0	2	0	5	0	0	0	0	0	0	0	0	0	0	0	34
.320	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0	6	11
.322	0	4	2	21	0	0	0	3	55	0	12	0	0	1	2	0	0	0	1	0	0	14	115
.324	0	2	0	2	0	0	0	0	1	1	4	0	0	0	2	1	0	0	0	0	0	0	13
.326	0	0	1	2	0	0	0	0	3	0	17	0	0	0	1	1	0	0	2	0	2	2	31
.328	0	3	2	3	2	0	0	3	16	1	6	0	0	1	0	5	3	2	6	0	2	0	55
12.002	0	0	7	12	0	0	0	0	0	0	4	0	0	0	0	8	0	0	3	0	2	1	37
.004	0	0	13	69	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	85
.006	0	0	6	22	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	1	0	33
.008	0	0	24	45	0	0	0	10	0	0	8	0	0	0	0	0	0	0	1	0	0	0	88
.010	0	0	18	73	0	0	0	22	0	0	4	0	0	0	0	0	0	0	0	0	0	4	121
.012	0	0	8	12	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31
.014	0	0	7	13	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	23
.016	0	0	20	38	0	0	0	4	0	0	7	0	0	0	0	0	0	0	0	0	0	0	69
.018	0	0	60	65	0	0	0	6	0	0	6	0	0	0	0	0	0	0	0	0	0	0	137
.020	0	0	8	60	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	74
.022	0	0	1	13	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	16
.024	0	0	24	72	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	97
.026	0	0	29	80	0	0	0	9	0	0	2	1	0	0	0	0	0	0	0	0	0	0	121
.028	0	0	6	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	1	13
.030	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	24
.032	0	0	10	6	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	20
.033	63	0	21	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	87
.035	0	0	14	6	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	23
.037	0	0	22	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	36
.039	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
.041	0	0	107	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	108
.043	0	0	82	2	0	0	3	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	94
.045	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33
.047	0	0	48	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	61
.049	0	0	53	7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	61
.051	0	0	35	13	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	51
.053	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
.055	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
.057	0	0	2	32	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	37

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
12.059	0	0	0	26	0	0	5	0	0	0	56	0	0	0	0	7	0	0	0	0	0	5	99
.061	0	0	0	32	0	0	1	0	0	0	5	0	0	0	0	2	0	0	1	0	0	0	41
.063	0	0	0	104	0	0	1	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	109
.065	0	0	0	555	0	0	3	0	2	0	25	0	0	0	2	17	4	2	2	0	1	1	614
.067	0	0	4	337	0	0	0	0	0	0	17	1	0	0	0	4	0	0	0	0	0	3	366
.069	0	0	0	195	0	0	0	0	2	0	14	0	0	1	0	6	3	1	4	0	1	0	227
.071	0	0	2	25	0	1	0	0	0	0	15	0	2	0	6	11	0	4	0	0	2	3	71
.075	0	0	16	204	0	1	0	0	12	2	11	0	0	0	10	11	3	0	2	3	1	18	294
.077	0	0	6	65	0	0	0	0	7	0	1	0	0	2	4	10	6	0	0	3	0	6	110
.079	0	0	18	80	0	0	0	1	0	0	5	0	0	0	12	10	0	0	0	0	0	3	129
.081	0	3	7	103	0	0	0	0	9	0	37	0	0	0	11	16	2	7	1	0	0	193	389
.084	0	0	27	127	0	0	0	2	2	0	30	0	0	0	1	13	0	3	0	0	1	1	207
.087	0	0	3	38	0	0	0	0	0	0	12	1	0	1	2	2	0	0	0	1	4	0	64
.090	0	0	1	5	0	0	0	0	0	0	7	0	0	0	0	4	0	0	0	0	1	0	18
.092	0	0	0	12	0	0	0	2	12	0	20	0	0	0	6	0	13	0	0	0	5	1	71
.094	0	0	5	62	0	0	13	25	42	0	140	0	0	0	34	35	0	0	3	11	0	7	377
.097	0	0	0	36	0	0	0	3	3	0	27	0	0	0	9	0	3	0	0	0	0	20	101
12.100	0	0	4	33	0	0	1	0	0	0	5	0	0	0	3	0	2	1	0	1	4	2	56
.103	0	0	6	67	0	0	2	2	0	0	35	0	0	0	3	0	1	0	0	5	0	3	124
.106	0	0	10	277	0	0	0	0	0	0	25	0	0	0	0	0	0	1	0	4	2	0	319
.109	0	0	4	41	0	0	0	0	0	0	8	0	0	0	3	0	0	0	0	7	0	2	65
.112	0	0	1	25	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	3	32
.115	0	0	0	48	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	2	0	5	72
.118	0	0	12	7	0	0	1	4	0	0	54	0	0	0	2	6	0	0	20	1	0	0	107
.120	0	0	5	1	0	0	0	0	0	0	7	0	0	0	0	0	0	0	2	0	0	0	15
.122	0	8	14	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	0	0	0	30
.124	0	8	5	0	0	0	0	1	0	0	6	1	0	1	1	0	0	0	3	0	0	3	29
.126	0	28	19	0	0	0	0	2	2	1	14	0	0	0	3	0	0	0	39	0	0	0	108
.128	0	2	28	0	0	0	0	2	0	0	6	0	0	0	1	1	0	0	8	0	0	1	49
.130	0	5	2	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	2	0	0	0	12
.132	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	1	0	8
.134	0	10	2	0	0	0	0	1	0	0	2	0	0	0	0	3	0	0	1	0	0	1	20
.136	0	6	3	0	1	0	1*	0	1	1	3	0	0	0	1	0	1	0	0	0	1	0	19
.138	0	0	1	1	0	0	0	0	1	0	2	0	0	0	2	1	0	0	1	0	0	1	10
.140	0	0	6	0	2	0	0	0	0	0	3	48	0	0	3	3	0	0	3	0	1	0	69
.142	0	19	11	0	2	7	0	1	5	0	4	3	0	0	3	5	2	0	7	9	0	6	84
.144	0	4	21	0	4	14	0	0	10	0	0	0	0	0	2	1	4	0	3	3	2	4	72
.146	0	0	2	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	11
.148	0	0	5	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	2	11
.150	0	0	47	0	0	0	0	1	0	8	13	11	0	0	0	0	1	0	0	0	0	5	86
.152	0	0	7	0	0	1	0	1	0	0	1	22	0	0	0	0	0	0	0	3	0	2	37
.154	0	3	0	0	0	4	0	0	0	2	1	0	0	0	0	0	0	0	1	0	1	0	12
.156	0	1	2	0	0	0	1*	0	1	0	4	2	0	0	1	0	0	0	0	0	2	0	14
.158	0	7	6	0	0	0	0	2	7	0	5	6	0	0	4	0	0	0	2	0	0	2	41
.160	0	0	1	0	0	0	0	0	5	2	2	3	0	0	2	0	0	0	0	0	0	4	19
.162	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5
.164	0	11	7	0	0	0	0	1	3	0	6	0	0	0	1	1	0	0	2	0	3	1	36
.184	0	1	15	0	0	1	0	0	1	0	10	0	0	0	2	0	0	0	14	1	0	0	45
.186	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	5
.188	0	0	3	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	8

Appendix Table 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
12.190	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	6
.192	0	13	1	0	0	0	0	0	2	1	5	4	0	0	1	8	0	0	9	0	1	0	45
.194	0	1	0	0	0	0	0	0	0	0	8	3	0	0	1	1	0	0	1	0	0	1	16
.196	0	2	5	0	0	0	0	0	0	1	9	0	0	1	0	0	0	0	3	0	0	1	22
.198	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0	5	0	0	2	0	1	0	12
12.200	0	0	0	1	0	0	0	1	1	0	13	0	0	0	0	5	0	1	12	0	1	1	36
.203	0	0	0	80	0	0	0	0	0	0	10	0	0	0	0	0	0	0	1	0	0	0	91
.206	0	0	0	10	0	0	0	0	0	0	21	0	0	0	0	0	0	1	0	0	1	3	36
.209	0	0	0	28	0	0	0	1	0	0	35	0	0	0	0	2	0	1	0	1	0	2	70
.212	0	0	13	92	0	0	0	0	0	0	176	0	0	0	1	6	0	5	0	1	0	6	300
.215	0	0	7	92	0	0	0	1	0	0	98	0	0	0	0	0	0	0	0	2	0	2	202
.218	0	0	4	22	0	0	11	4	2	0	61	0	0	0	6	0	12	0	0	0	2	3	127
.221	0	0	2	102	0	0	2	3	13	0	47	0	0	0	18	0	5	0	5	1	0	11	209
.224	0	0	5	315	0	0	5	63	39	0	471	0	1	0	105	6	30	0	6	5	0	38	1089
.227	0	1	6	98	0	0	1	5	4	0	30	0	0	0	10	0	2	0	0	0	1	4	162
.230	0	0	1	22	0	0	1	1	1	0	16	0	0	0	2	3	0	1	1	0	0	0	49
.233	0	0	3	126	0	0	1	0	0	0	107	0	0	2	2	4	0	1	0	1	2	1	250
.235	0	0	0	194	0	0	1	1	0	0	61	0	0	0	3	17	1	1	1	0	0	0	280
.238	0	0	2	145	0	0	0	1	0	0	42	0	0	3	16	11	4	0	1	0	0	0	225
.240	0	0	0	23	0	0	0	1	5	0	5	0	0	1	8	2	3	0	0	0	0	6	54
.242	0	0	0	14	0	0	0	0	3	0	1	0	0	0	1	2	0	1	0	2	1	0	25
.244	0	0	10	17	0	0	0	1	17	2	10	0	0	0	7	15	0	3	12	8	0	3	105
.246	0	0	7	205	0	0	1	0	0	0	16	0	0	0	0	2	2	0	2	4	3	6	248
.248	0	0	0	43	0	0	0	0	0	0	5	0	0	0	0	2	0	0	0	0	0	1	51
.250	0	0	6	38	0	0	1	0	0	0	6	0	0	0	0	2	0	0	0	0	0	1	54
.252	0	0	7	13	0	0	0	0	0	0	12	0	0	0	0	6	0	1	5	0	0	0	44
.254	0	0	9	22	0	0	0	0	0	0	16	0	0	0	0	1	0	1	35	0	0	0	84
.256	0	0	5	11	0	0	0	0	0	0	2	0	0	0	0	0	0	1	3	0	1	0	23
.258	0	0	0	38	0	0	1	0	0	0	1	0	0	0	0	2	0	0	1	0	0	0	43
.260	0	0	0	26	0	0	0	0	0	0	40	0	0	0	2	6	0	0	0	0	0	0	74
.262	0	0	127	24	0	0	0	1	0	0	2	0	0	0	0	0	0	0	7	0	0	0	161
.264	0	1	3	15	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	0	2	26
.265	0	0	17	31	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	4	54
.268	0	0	57	44	0	0	0	54	0	0	1	0	0	0	0	0	0	0	0	0	0	0	156
.270	0	0	12	35	0	0	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	1	60
.272	0	0	1	61	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	3	0	81
.274	0	1	17	25	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	2	0	85
.276	0	0	7	8	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	1	20
.278	0	0	6	19	0	0	0	13	0	0	7	0	0	0	0	0	0	0	0	0	0	0	45
.280	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5
.282	0	0	0	5	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	8
.284	0	0	0	10	0	0	0	3	0	1	2	0	0	0	0	0	0	0	0	0	0	0	16
13.001	0	0	0	31	0	0	0	0	0	0	6	0	0	0	0	0	1	0	0	1	2	0	41
.003	0	3	0	315	0	0	0	0	0	0	34	0	0	0	0	12	0	0	8	10	3	0	385
.005	0	0	0	1020	0	0	3	0	0	0	21	0	0	0	0	24	2	0	2	1	2	0	1075
.007	0	0	0	115	0	0	1	0	0	0	6	0	0	0	1	7	0	0	2	0	1	0	133
.009	0	0	0	470	0	0	0	0	0	0	21	0	0	0	0	0	1	0	0	0	2	0	494
.011	0	0	0	372	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	374

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	*Benthosema panamense*	*Ceratoscopelus townsendi*	*Diaphus* spp.	*Diogenichthys laternatus*	*Diogenichthys atlanticus*	*Electrona* sp.	*Gonichthys tenuiculus*	*Hygophum atratum*	*Hygophum proximum*	*Lampadena* spp.	*Lampanyctus* spp.	*Lepidophanes pyrsobolus*	*Lobianchia* sp.	*Loweina rara*	*Myctophum* spp.	*Notolychnus valdiviae*	*Notoscopelus resplendens*	*Protomyctophum* sp.	*Symbolophorus evermanni*	*Triphoturus* spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
13.013	0	0	0	186	0	0	1	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	207
.015	0	0	0	477	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	479
.017	0	0	0	550	0	0	2	0	0	0	5	0	0	0	0	1	0	0	1	0	0	0	559
.019	482	0	0	715	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	13	1219
.021	407	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	409
.022	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.028	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.030	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24
.032	0	0	0	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
.034	0	0	0	142	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	158
.036	0	0	0	11	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	13
.038	0	0	0	122	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	2	142
.040	0	0	0	408	0	0	3	0	0	0	47	0	0	0	0	1	1	6	1	0	0	2	469
.042	0	0	0	271	0	0	0	0	0	0	25	0	0	1	0	3	0	6	0	0	0	1	307
.044	0	0	0	79	0	0	0	0	1	0	14	0	0	0	2	7	1	3	1	0	1	0	109
.046	0	0	0	44	0	0	1	0	0	0	28	0	1	0	2	8	0	3	7	1	4	6	105
.048	0	0	1	160	0	0	4	0	3	0	76	3	2	0	5	19	0	4	9	10	2	2	300
.050	0	0	1	71	0	0	2	0	1	0	25	7	1	0	2	11	1	2	4	4	1	0	133
.052	0	0	0	42	0	0	0	0	0	0	14	0	1	1	1	5	0	0	4	4	5	2	79
.054	0	0	0	36	0	0	1	0	0	0	20	0	3	0	0	12	0	0	2	0	3	0	77
.056	0	0	3	33	0	0	0	0	8	0	43	0	2	1	5	8	0	0	4	12	21	4	144
.058	0	0	2	50	0	0	3	0	0	0	16	0	0	1	0	1	0	0	0	5	5	0	83
.060	0	0	0	54	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	2	59
.062	0	0	4	22	0	0	1	3	0	0	7	0	0	0	0	0	1	0	0	3	2	1	44
.064	0	0	5	191	0	0	15	2	1	0	18	0	0	0	6	1	21	1	0	10	3	0	274
.065	0	0	1	12	0	0	2	1	1	0	8	0	0	0	1	0	1	1	0	1	0	2	31
.067	0	0	2	24	0	0	2	0	0	0	2	0	0	0	0	0	3	0	0	0	0	1	34
.069	0	0	2	73	0	0	2	0	0	0	10	0	0	1	0	0	5	0	0	2	1	3	99
.071	0	0	0	284	0	0	6	0	0	0	20	0	0	0	0	0	0	0	2	5	0	1	318
.073	0	0	0	122	0	0	3	0	0	0	40	0	0	0	0	0	0	0	2	5	0	0	172
.075	0	0	0	28	0	0	2	0	0	0	5	0	0	0	0	0	0	0	1	0	0	3	39
.077	0	0	0	60	0	0	1	0	0	0	23	0	0	0	0	0	0	0	1	3	0	1	89
.079	0	0	0	50	0	0	1	0	0	0	8	0	0	0	0	1	0	0	7	2	0	0	69
.081	0	0	0	11	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	1	0	0	16
.083	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	17
.085	0	0	0	9	0	0	0	0	0	0	2	0	0	0	0	0	0	0	6	0	0	0	17
.087	0	9	0	0	0	0	0	3	0	0	0	0	0	0	0	4	0	0	18	0	1	2	37
.089	0	25	1	0	0	0	0	2	0	0	3	0	0	0	0	7	0	0	34	0	32	1	105
.091	0	13	12	0	0	0	0	10	0	0	0	0	0	0	1	1	0	0	8	0	0	4	49
.093	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	2	0	0	2	8
.095	0	45	11	1	2*	0	0	45	3	0	7	0	0	1	15	21	4	0	30	3	3	4	195
.097	0	20	21	0	18	2	1	33	4	0	3	1	4	0	18	37	7	0	24	6	5	1	205
.099	0	15	4	0	2	0	0	5	2	0	1	0	0	0	0	7	0	0	5	6	1	0	48
13.101	0	6	10	0	1	0	0	6	0	0	0	0	0	0	3	4	0	0	10	5	0	0	45
.103	0	29	46	9	12*	3	0	42	9	0	19	0	4	0	11	16	13	0	26	6	10	0	255
.105	0	30	19	0	6	3	0	22	3	0	5	0	0	0	5	7	0	0	33	24	4	5	166
.107	0	2	1	0	0	0	0	2	1	0	1	0	0	0	2	0	0	0	1	0	2	1	13
.109	0	1	15	0	0	1	0	2	2	0	1	0	0	0	0	1	0	0	1	1	1	1	27
.111	0	6	17	0	0	1	0	5	0	0	3	1	1	0	7	2	1	0	0	4	0	1	49
.113	0	17	26	0	4	1	0	1	0	7	5	1	0	0	1	1	0	0	2	2	2	2	72

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
13.115	0	2	4	0	4	2	1*	0	0	2	0	0	0	0	3	1	0	0	0	0	4	2	25
.117	0	2	20	0	0	0	0	0	0	18	7	0	0	1	1	0	0	0	0	0	3	0	52
.119	0	7	56	0	0	2	0	3	0	6	3	1	0	0	0	0	0	0	0	4	4	0	86
.121	0	6	1	0	0	1	1*	4	0	1	2	0	0	0	1	2	0	0	0	0	2	1	22
.123	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
.125	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2
.127	0	7	3	0	0	3	2*	4	4	3	5	0	1	0	1	4	0	0	0	0	2	0	39
.129	0	7	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	1	0	2	0	14
.131	0	2	1	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	7
.133	0	2	1	0	0	0	0	0	0	2	1	0	0	0	1	0	0	0	0	0	0	2	9
.135	0	12	35	0	0	1	1*	0	1	11	7	0	1	0	0	0	0	0	0	5	2	2	78
.137	0	5	13	0	0	3	0	2	0	2	6	0	0	0	2	6	0	0	0	9	0	2	50
.139	0	0	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	2	8
.141	0	1	0	0	1	0	0	0	0	0	1	0	0	0	3	1	0	0	0	0	0	1	8
.143	0	15	21	0	6	2	0	4	0	5	7	2	0	0	5	1	0	0	1	13	2	2	86
.145	0	16	6	0	4	0	0	2	0	0	4	0	0	0	0	2	2	0	0	8	0	0	44
.147	0	2	5	0	2	2	0	0	0	0	2	0	0	0	3	2	3	0	1	10	0	1	33
.149	0	2	2	0	2	0	0	1	0	0	1	2	0	0	3	5	0	0	5	3	1	2	29
.151	0	43	6	0	2	0	0	0	0	4	0	3	0	0	2	1	0	0	1	8	1	1	72
.153	0	83	172	0	7	0	0	30	23	0	9	0	0	0	7	26	1	0	11	8	3	14	394
.155	0	4	2	0	0	2	0	0	0	0	0	0	0	0	0	4	0	0	4	0	0	0	16
.157	0	11	19	0	1	1	0	4	0	0	0	0	0	0	0	2	0	0	1	2	0	4	45
.159	0	12	16	0	0	0	0	3	0	0	1	0	0	0	0	7	0	0	7	0	2	5	53
.161	0	27	11	0	1	0	0	4	1	0	4	0	0	0	0	4	0	0	10	0	1	2	65
.163	0	1	2	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	6	0	0	1	14
.165	0	3	6	0	0	0	0	0	0	0	0	0	1	0	2	3	0	0	8	0	0	1	24
.167	0	16	2	0	0	0	0	2	0	0	3	0	0	0	1	0	0	0	8	0	1	0	33
.169	0	115	1	8	0	0	0	2	0	0	20	1	0	0	0	1	0	0	17	0	0	4	169
.171	0	5	13	54	0	0	1	0	0	0	7	0	0	0	0	2	0	0	8	0	3	11	104
.173	0	2	0	98	0	0	0	0	0	0	13	0	0	1	0	0	0	0	2	0	1	4	121
.175	0	0	1	168	0	0	0	1	0	0	52	0	0	1	2	0	0	0	18	0	2	0	245
.179	0	0	0	122	0	0	1	0	0	0	7	0	0	0	2	0	0	0	0	1	0	0	133
.183	0	0	0	64	0	0	3	0	0	0	7	0	0	1	2	0	0	0	0	2	0	1	80
.187	0	0	0	49	0	0	2	0	0	0	11	0	0	0	0	0	1	0	0	3	0	1	67
.191	0	0	0	78	0	0	2	0	0	0	43	0	0	0	0	0	0	0	0	3	0	0	126
.195	0	0	4	34	0	0	0	0	0	0	125	0	0	2	0	0	0	0	1	16	0	0	182
.199	0	0	1	31	0	0	4	2	0	0	12	0	0	0	3	0	2	0	0	0	0	0	55
13.203	0	0	0	7	0	0	1	3	0	0	3	0	0	0	4	0	0	0	1	0	0	1	20
.207	0	0	1	72	0	0	12	8	1	0	24	0	0	1	2	1	0	0	0	4	0	3	129
.211	0	0	3	40	0	0	5	1	0	0	9	0	0	0	3	1	0	0	0	2	4	0	68
.215	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	7
.219	0	0	0	6	0	0	1	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	11
.223	0	0	0	18	0	1	0	0	0	0	9	0	0	0	0	1	0	0	0	2	1	0	32
.227	0	0	2	90	0	0	1	0	3	0	15	0	0	0	0	2	0	0	1	1	6	0	121
.231	0	0	0	29	0	0	2	0	0	0	39	0	0	0	4	3	1	0	0	0	2	2	82
.235	0	0	1	64	0	1	3	0	0	0	14	0	0	1	5	7	0	3	0	1	1	5	106
.237	0	0	0	133	0	0	0	0	0	4	34	0	0	0	0	8	0	1	1	2	1	5	189
.239	0	0	0	131	0	0	1	0	0	0	29	0	0	0	0	7	0	4	2	5	0	0	179
.241	0	0	0	52	0	0	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	2	59
.243	0	0	0	67	0	0	0	0	0	1	21	0	0	0	0	0	0	0	0	1	0	3	93

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	*Benthosema panamense*	*Ceratoscopelus townsendi*	*Diaphus* spp.	*Diogenichthys laternatus*	*Diogenichthys atlanticus*	*Electrona* sp.	*Gonichthys tenuiculus*	*Hygophum atratum*	*Hygophum proximum*	*Lampadena* spp.	*Lampanyctus* spp.	*Lepidophanes pyrsobolus*	*Lobianchia* sp.	*Loweina rara*	*Myctophum* spp.	*Notolychnus valdiviae*	*Notoscopelus resplendens*	*Protomyctophum* sp.	*Symbolophorus evermanni*	*Triphoturus* spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
13.245	0	0	0	37	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	57
.247	0	0	0	17	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	26
.249	0	0	0	43	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	46
.251	0	0	0	15	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	25
.253	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6
.255	12	0	11	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	2	0	29
.257	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	10
.259	0	0	16	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	4	23
.261	0	0	8	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	13
.263	0	0	33	5	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	46
.265	0	0	11	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	14
.266	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
.268	0	0	12	19	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33
.270	0	0	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	9
.272	0	0	11	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	13
.274	0	0	26	33	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	63
.276	0	0	38	48	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	89
.278	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	7
.280	0	0	23	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	31
.282	0	0	80	7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	89
.284	0	0	13	7	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	1	0	34
13.318	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
.320	3	0	11	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
.322	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.324	0	0	0	25	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26
.326	0	0	5	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
.328	0	0	0	28	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	35
.330	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24
.332	0	0	0	62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	63
.334	0	0	0	111	0	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	116
.338	0	0	0	274	0	0	0	0	0	0	15	0	0	0	0	1	0	1	0	2	1	1	295
.340	0	0	0	33	0	0	0	0	0	0	5	0	0	0	3	3	0	1	0	1	1	0	47
.342	0	0	0	62	0	0	0	0	0	0	6	0	0	0	2	3	0	0	0	1	1	1	76
14.001	46	0	0	725	0	0	1	0	0	0	49	0	0	0	18	0	0	0	5	17	0	6	867
.006	0	0	9	43	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	2	8	0	66
.008	0	0	0	78	0	0	0	0	0	0	3	0	0	0	5	0	0	0	0	0	0	0	86
.010	0	0	6	179	0	0	0	2	0	0	4	0	0	0	6	0	0	0	0	0	0	1	198
.012	0	0	0	47	0	0	0	0	0	0	2	0	0	0	7	0	0	0	0	0	0	1	57
.014	0	0	1	65	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	67
.016	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
.017	0	0	0	54	0	0	1	0	0	0	1	0	0	0	4	0	0	0	0	0	0	1	61
.018	0	0	0	246	0	0	1	0	0	0	148	0	0	0	23	0	0	0	4	1	0	1	424
.020	0	0	0	225	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1	0	229
.022	0	0	1	73	0	0	0	0	0	0	3	0	0	0	2	0	0	0	1	0	0	0	80
.024	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	47
.027	0	0	0	372	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	4	387
.029	0	0	5	371	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	382
.031	0	0	4	540	0	0	1	1	0	0	19	0	0	0	13	0	0	0	6	2	1	7	594

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I.—*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
14.033	0	0	0	21	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	2	26
.040	0	0	1	16	0	0	4	0	0	0	5	0	0	0	9	0	0	0	0	1	0	0	36
.043	0	0	4	25	0	0	9	0	0	0	40	0	0	0	41	0	25	0	2	3	1	9	159
.047	0	0	0	9	0	0	0	0	0	0	4	0	0	0	8	0	0	0	0	1	0	0	22
.051	0	0	0	31	0	0	0	0	0	0	27	0	0	0	12	0	0	0	1	1	0	6	78
.055	0	0	0	37	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	40
.060	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	18
.066	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.069	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.076	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.078	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.081	0	0	0	5	0	0	0	0	0	0	8	0	0	0	0	0	0	0	3	1	0	1	18
.084	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
.086	0	0	0	1	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	1	7
.088	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
.091	0	1	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0	1	1	0	0	43
.095	0	0	0	17	0	0	0	0	0	0	1	0	0	0	0	0	1	0	19	0	0	12	50
.099	0	0	0	7	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	1	15
14.103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.110	0	0	0	6	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	1	0	6	27
.112	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
.114	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
.115	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	1	0	0	0	5
.117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
.118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.120	0	0	1	5	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	4	2	0	15
.122	0	0	0	7	0	0	0	0	0	0	1	0	0	0	0	0	1	0	8	1	0	1	19
.123	0	0	0	7	1	0	1	6	0	0	4	1	0	0	0	1	0	0	16	1	0	13	51
.124	0	6	4	15	1	0	0	40	0	0	18	0	0	1	2	1	2	0	51	1	10	0	152
.126	0	1	3	0	0	0	0	5	0	0	1	0	0	0	5	3	0	0	21	1	0	13	53
.127	0	1	1	0	0	0	1	2	0	0	1	0	0	0	1	0	0	0	5	9	0	1	22
.128	0	3	10	2	0	0	0	33	0	0	5	2	0	0	0	4	3	0	72	9	2	0	145
.130	0	0	1	7	0	0	0	1	0	0	0	3	0	0	5	2	0	0	21	0	0	5	45
.131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
.132	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	3	1	0	1	8
.134	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	11
.136	0	0	0	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43
.138	0	0	0	15	0	0	1	0	0	0	11	0	0	0	0	0	0	0	0	2	0	0	29
.142	0	0	0	108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	110
.146	0	0	0	152	0	0	5	0	0	0	13	0	0	0	0	0	0	0	0	6	0	0	176
.150	0	0	0	39	0	0	0	0	0	0	6	0	0	0	0	0	0	0	2	0	0	5	52
.154	0	0	2	12	0	0	0	0	0	0	49	0	0	0	16	0	0	0	8	2	3	0	92
.158	0	0	0	17	0	0	0	0	0	0	7	0	0	0	2	0	0	0	0	0	0	4	30
.164	0	0	0	76	0	0	1	0	0	0	30	0	0	0	5	0	1	0	0	2	0	20	135
.172	0	0	0	16	0	0	2	0	0	0	6	0	0	0	0	0	1	0	0	1	0	0	26
.174	0	0	4	11	0	0	1	0	0	0	4	0	0	0	2	3	0	0	1	0	0	0	26
.177	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.183	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	4
.188	0	0	0	181	0	0	3	0	0	0	49	0	0	0	6	2	9	0	5	6	0	0	261

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on EASTROPAC I. —*Continued.*

STATION NUMBER	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Diogenichthys atlanticus	Electrona sp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes pyrsobolus	Lobianchia sp.	Loweina rara	Myctophum spp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified myctophids	Disintegrated myctophids	Total myctophids
14.194	0	0	0	1551	0	0	7	0	0	0	158	0	0	2	12	4	8	0	5	5	1	0	1753
.195	0	0	0	243	0	0	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	4	252
.199	0	0	1	10	0	0	0	0	0	0	2	0	0	0	0	1	0	0	2	0	0	0	16
14.203	0	0	0	90	0	0	1	0	0	0	65	0	0	0	3	1	3	0	4	4	1	7	179
.209	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	25
.213	0	0	0	181	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	206
.218	0	0	0	168	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	1	0	0	177
.220	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	22
.220	0	0	0	46	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	49
.224	0	0	0	90	0	0	0	0	0	0	21	0	0	0	0	0	0	0	2	0	0	2	115
.228	0	0	0	28	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	30
.230	0	0	0	39	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	41
.232	0	0	0	21	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	1	0	0	31
.234	0	0	0	98	0	0	0	0	0	0	81	0	0	0	0	0	0	0	0	0	1	48	228
.236	0	0	0	30	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	34
.240	0	0	0	70	0	0	4	0	0	0	12	0	0	1	20	2	2	0	1	1	0	3	116
.243	0	0	0	23	0	0	2	0	0	0	14	0	0	0	2	0	2	0	0	0	0	1	44
.247	0	0	0	41	0	0	3	0	0	0	27	0	0	0	5	0	2	0	1	6	0	1	86
.251	0	0	0	19	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	1	1	0	25
.255	0	0	1	216	0	0	1	0	0	0	2	0	0	0	3	0	0	0	0	3	1	0	227
.259	0	0	0	46	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	3	1	53
.263	0	0	0	94	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	1	0	0	105
.267	0	0	0	4	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	0	8
.276	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	6	0	2	1	13
.280	0	0	0	6	0	0	2	0	0	0	2	0	0	0	0	0	0	0	26	3	0	5	44
.283	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	1	0	22
.287	0	0	0	3	0	0	0	0	0	0	4	0	0	0	0	0	0	0	1	2	4	1	15
.291	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.295	0	0	0	49	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	1	0	65
.300	0	0	0	16	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	18
.303	0	0	0	189	0	0	0	0	0	0	5	0	0	0	3	0	0	0	0	3	0	0	200
.306	0	0	0	27	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	0	32
.310	0	0	1	61	0	0	2	0	0	0	8	0	0	1	5	0	4	0	0	14	0	0	96
.314	0	0	0	38	0	0	0	0	0	0	14	0	0	0	5	0	0	0	0	0	2	0	59
.318	0	0	0	491	0	0	7	0	0	0	38	0	0	0	23	0	5	0	0	2	0	0	566
.323	0	0	8	149	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3	3	165
.326	0	0	3	573	0	0	0	0	0	0	73	0	0	0	1	0	0	0	0	4	0	5	659
.330	0	0	0	22	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	23

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia spp.	Araiophos sp.	Cyclothone spp.	Diplophos sp.	Ichthyococcus spp.	Maurolicus muelleri	Vinciguerria spp.	Bathophilus filifer	Evermannellidae	Macroparalepis macrurus	Sudis atrox	Scopelo saurus spp.	Oxyporhamphus micropterus	Trachypteridae	Auxis spp.	Katsuwonis pelamis	Coryphaena spp.	Naucrates ductor	Howella pammelas	Tetragonurus sp.	Ceratioidei
11.022	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.025	0	0	0	0	6	0	0	0	46	0	0	1	0	0	0	0	0	0	0	0	0	0	0
.027	0	0	0	0	2	0	0	0	34	0	1	1	0	0	0	0	0	0	0	0	0	0	0
.030	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.032	1	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.034	1	0	0	0	0	0	0	0	88	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.036	0	0	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.038	4	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.040	0	0	0	0	1	1	0	0	18	0	0	0	0	0	0	1	0	0	0	0	0	0	1
.044	2	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.046	3	0	0	0	1	0	0	0	57	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.048	12	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.050	24	0	0	0	1	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.052	15	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.054	11	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.056	10	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.058	10	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0
.060	13	0	0	0	1	0	1	0	7	0	0	1	0	0	0	0	3	0	1	0	0	0	0
.062	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.064	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
.066	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	2	1	1	0	11	0	1
.068	5	0	0	0	6	1	0	0	70	0	0	1	0	0	0	0	0	0	3	0	3	0	4
.070	1	0	0	0	6	1	0	0	17	0	3	1	0	0	1	0	0	0	0	0	8	0	1
.072	2	0	2	0	6	2	0	0	65	0	0	0	0	0	0	0	0	0	1	0	9	0	1
.076	6	0	0	0	5	0	2	0	682	1	1	0	0	0	0	0	0	4	0	0	0	0	0
.080	7	0	0	0	2	1	0	0	139	3	0	1	0	0	0	0	0	0	0	0	0	0	0
.084	11	0	0	0	3	0	0	0	358	0	0	0	0	0	0	0	3	0	0	0	2	0	0
.088	1	0	0	0	9	0	0	0	315	1	0	1	0	0	0	0	0	0	1	0	2	0	0
.094	0	0	0	0	9	0	0	0	41	0	0	0	0	0	0	1	0	0	1	0	1	0	2
.098	2	0	0	0	20	0	0	0	87	0	0	0	0	0	0	0	0	1	0	0	0	0	1
11.102	6	0	3	0	8	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	2	0	0
.106	1	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	4	0	2
.110	8	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.114	1	0	0	0	11	2	0	0	44	0	0	0	0	0	0	0	0	0	0	0	3	0	1
.118	4	0	0	0	1	2	0	0	4	0	0	0	0	0	0	0	0	0	0	0	2	0	0
.120	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
.124	0	0	0	0	7	1	0	0	17	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.128	0	0	0	0	6	0	0	0	92	0	0	0	0	0	0	0	0	0	0	0	2	0	1
.130	0	0	0	0	6	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.132	0	0	0	0	5	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0
.134	0	0	0	0	3	24	0	0	1	0	0	0	0	0	0	1	0	166	0	0	0	2	0
.136	0	0	0	0	24	2	0	0	20	0	0	0	0	0	0	0	0	2	0	0	0	0	0
.138	0	0	1	0	6	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.140	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.142	0	0	0	0	9	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	0
.146	0	0	0	20	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
.148	0	0	0	61	15	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.150	0	0	0	70	11	0	0	0	1	0	0	0	0	0	0	0	0	4	0	0	0	0	0
.152	0	0	0	89	38	1	0	0	9	0	0	0	1	0	0	0	0	1	1	0	2	1	0
.154	0	0	2	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.156	0	0	0	83	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.158	0	0	0	20	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.159	0	0	0	70	24	0	0	0	6	0	0	0	3	0	0	0	0	0	0	0	0	0	0
.161	0	0	0	0	10	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia spp.	Araiophos sp.	Cyclothone spp.	Diplophos sp.	Ichthyococcus spp.	Maurolicus muelleri	Vinciguerria spp.	Bathophilus filifer	Evermannellidae	Macroparalepis macrurus	Sudis atrox	Scopelo saurus spp.	Oxyporhamphus micropterus	Trachypteridae	Auxis spp.	Katsuwonis pelamis	Coryphaena spp.	Naucrates ductor	Howella pammelas	Tetragonurus sp.	Ceratioidei
11.163	0	0	0	0	8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.167	0	0	0	0	25	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0
.169	0	0	0	0	3	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
.171	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.173	0	0	0	0	9	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
.175	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.177	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.179	0	0	0	0	4	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
.181	0	0	0	0	13	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
.183	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.185	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.187	0	0	0	0	19	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0
.189	0	0	0	0	20	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.191	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.195	0	0	0	4	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.197	0	0	0	8	32	0	0	0	5	0	2	0	1	0	0	0	1	1	0	0	3	0	0
.199	0	0	0	5	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
11.201	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
.203	0	0	0	8	12	0	0	0	3	0	2	1	0	0	0	0	0	0	0	0	0	0	0
.205	0	0	0	22	20	0	2	0	9	3	0	0	0	0	0	0	0	0	0	0	0	0	0
.207	0	0	0	10	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.209	0	0	0	3	3	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
.211	0	0	0	35	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
.213	0	0	0	13	10	1	0	0	12	0	0	0	0	0	0	0	1	3	0	0	1	0	0
.215	0	0	0	3	2	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	1	0	0
.217	0	0	0	0	3	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0	0	0	1
.219	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.221	0	0	0	0	18	2	0	0	36	0	0	0	0	0	0	0	1	0	1	0	0	0	0
.223	0	0	0	0	8	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.226	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.228	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.234	2	0	0	0	7	2	0	0	8	0	0	0	0	0	0	1	0	0	2	0	1	1	1
.238	0	0	0	0	3	0	0	0	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0
.242	4	0	0	0	13	0	1	0	36	0	0	0	0	0	0	0	0	0	0	0	4	0	0
.246	2	0	0	0	15	0	0	0	36	0	0	0	0	0	0	0	0	0	1	0	1	0	1
.250	1	0	1	0	12	0	0	0	8	0	0	0	0	0	0	1	0	0	1	0	0	0	1
.254	0	0	0	0	5	0	0	0	15	1	0	1	0	0	1	0	0	0	0	0	2	0	0
.258	3	0	1	0	8	0	0	0	46	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.262	2	0	0	0	10	0	0	0	58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.266	3	0	0	0	3	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.270	4	0	0	0	1	0	0	0	17	0	0	0	0	0	0	0	7	0	0	0	1	0	0
.278	13	0	1	0	13	0	0	0	142	0	0	0	0	0	0	0	0	0	1	0	0	0	0
.282	1	0	0	0	6	0	1	0	20	0	1	0	0	0	0	0	0	0	1	0	0	0	0
.285	9	0	0	0	5	0	0	0	5	0	2	1	0	0	1	0	0	0	1	0	1	0	1
.287	1	0	0	0	4	0	0	0	14	0	1	2	0	0	0	0	0	0	0	0	2	0	2
.289	0	0	0	0	7	4	0	0	5	0	0	0	0	0	0	0	0	0	1	0	18	0	6
.291	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	4	0	0
.293	7	0	1	0	1	0	0	0	2	0	0	0	0	0	0	0	6	0	0	0	14	0	1
.295	10	0	0	0	5	0	0	0	10	0	0	0	0	0	0	1	0	1	1	0	3	0	2
.297	5	0	0	0	3	0	0	0	9	0	0	0	0	0	0	0	2	1	0	0	1	0	4
.299	27	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	1	0	1
11.301	1	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	1	0	1	0	0	0	3
.303	12	0	0	0	2	0	0	0	45	0	0	0	0	0	0	1	0	0	0	0	0	0	1
.306	4	0	0	0	0	0	0	0	64	0	0	0	0	0	0	0	1	0	0	0	0	0	1

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	*Bathylagus nigrigenys*	*Leuroglossus stilbius urotranus*	*Nansenia* spp.	*Araiophos* sp.	*Cyclothone* spp.	*Diplophos* sp.	*Ichthyococcus* spp.	*Maurolicus muelleri*	*Vinciguerria* spp.	*Bathophilus filifer*	Evermannellidae	*Macroparalepis macrurus*	*Sudis atrox*	*Scopelo saurus* spp.	*Oxyporhamphus micropterus*	Trachypteridae	*Auxis* spp.	*Katsuwonis pelamis*	*Coryphaena* spp.	*Naucrates ductor*	*Howella pammelas*	*Tetragonurus* sp.	Ceratioidei
11.308	1	0	0	0	2	0	0	0	4	0	0	0	0	0	0	0	0	0	2	0	0	0	1
.310	4	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.312	0	0	0	0	2	1	0	0	59	0	0	1	0	0	0	1	0	0	0	0	0	0	1
.314	5	0	0	0	0	0	0	0	32	1	0	0	0	0	0	0	0	0	1	0	0	0	0
.316	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0
.318	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.320	1	0	0	0	0	0	0	0	10	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.322	0	0	0	0	2	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.324	0	0	0	0	2	0	0	0	19	0	0	1	0	0	0	0	0	0	0	0	0	0	0
.326	0	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.328	0	0	0	0	9	0	0	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12.002	3	0	0	0	1	1	0	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.004	3	0	0	0	0	1	0	0	11	3	0	0	0	0	0	0	0	0	0	0	0	0	0
.006	2	0	0	0	0	3	0	0	12	5	0	0	0	0	0	0	0	0	2	0	0	0	0
.008	3	0	0	0	0	6	0	0	59	2	0	0	0	0	0	0	0	0	1	0	0	0	0
.010	8	0	0	0	0	1	0	0	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.012	4	0	0	0	0	8	0	0	16	1	0	0	0	0	0	0	0	0	1	0	0	0	0
.014	4	0	0	0	0	5	0	0	33	2	0	0	0	0	0	0	0	0	0	0	0	0	0
.016	8	0	0	0	0	4	0	0	178	4	0	0	0	0	0	1	0	0	0	0	0	0	2
.018	0	0	0	0	0	0	0	0	199	7	0	0	0	0	1	0	0	0	0	0	0	0	0
.020	3	0	0	0	0	3	0	0	20	4	0	0	0	0	0	0	0	0	1	0	0	0	0
.022	0	0	0	0	0	4	0	0	11	1	0	0	0	0	1	0	0	0	0	0	0	0	0
.024	3	0	0	0	0	8	0	0	234	32	0	0	0	0	0	0	0	0	0	1	0	0	0
.026	4	0	0	0	0	2	0	0	99	3	0	0	0	0	0	0	0	0	0	0	0	0	0
.028	0	0	0	0	0	1	0	0	31	0	0	0	0	0	2	0	3	0	0	0	0	0	1
.030	6	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	1	0	0	0	0	0	3
.032	0	0	0	0	0	0	0	0	13	1	0	0	0	0	0	0	7	0	0	0	0	0	3
.033	3	0	0	0	0	0	0	0	36	3	0	0	0	0	0	0	6	0	1	0	0	0	0
.035	1	0	0	0	0	1	0	0	72	4	0	0	0	0	5	0	2	0	0	0	0	0	2
.037	9	0	0	0	0	1	0	0	10	1	0	0	0	0	0	0	2	0	0	0	0	0	0
.039	4	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0
.041	3	0	0	0	0	2	0	0	20	3	0	0	0	0	3	0	1	0	0	0	0	0	0
.043	0	0	0	0	0	0	0	0	28	2	0	0	0	0	3	1	0	0	0	0	0	0	0
.045	0	0	0	0	0	0	0	0	7	0	0	0	0	0	3	0	0	0	0	0	0	0	0
.047	1	0	0	0	0	2	0	0	2	0	0	0	0	0	3	0	1	0	0	0	0	0	1
.049	2	0	0	0	0	2	0	0	52	1	0	0	0	0	0	0	2	0	0	0	0	0	0
.051	0	0	0	0	0	0	0	0	68	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.053	1	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	2	0	1	0	0	0	0
.055	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	2	0	0	0	0	0	0	0
.057	2	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.059	21	0	0	0	12	0	0	0	66	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.061	8	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.063	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.065	11	0	0	0	3	0	0	0	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.067	2	0	0	0	4	0	0	0	31	0	0	0	0	0	2	0	19	0	7	0	3	0	1
.069	5	0	0	0	6	0	1	0	11	0	0	0	0	0	0	1	2	0	1	0	7	0	0
.071	9	0	3	0	2	0	0	0	16	0	0	0	0	0	0	0	0	0	1	0	0	0	1
.075	19	0	2	0	6	0	1	0	119	1	2	1	0	0	2	0	0	0	1	0	1	0	2
.077	13	0	1	0	3	0	0	0	23	0	0	0	0	0	2	1	1	0	0	0	4	0	0
.079	17	0	1	0	24	0	0	2	21	0	0	0	0	0	2	0	42	0	0	0	3	0	2
.081	29	0	0	0	15	0	0	0	59	0	0	0	0	0	2	0	30	0	0	0	2	0	1
.084	14	0	0	0	5	0	0	0	6	0	0	0	0	0	0	0	8	0	0	0	0	0	0
.087	13	0	1	0	6	0	0	0	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia spp.	Araiophos sp.	Cyclothone spp.	Diplophos sp.	Ichthyococcus spp.	Maurolicus muelleri	Vinciguerria spp.	Bathophilus filifer	Evermannellidae	Macroparalepis macrurus	Sudis atrox	Scopelo saurus spp.	Oxyporhamphus micropterus	Trachypteridae	Auxis spp.	Katsuwonis pelamis	Coryphaena spp.	Naucrates ductor	Howella pammelas	Tetragonurus sp.	Ceratioidei
12.090	4	0	2	0	2	0	1	7	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.092	0	0	0	0	5	0	0	4	41	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.094	3	0	0	0	8	0	0	1	124	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.097	3	0	0	0	7	0	0	8	46	0	0	0	0	0	0	1	0	0	0	0	0	0	1
12.100	12	0	3	0	4	0	0	0	10	0	0	0	0	0	0	1	1	0	0	0	1	0	0
.103	0	0	0	0	3	0	0	1	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.106	26	0	5	0	6	0	0	0	35	0	0	0	0	0	1	1	3	0	0	0	0	0	0
.109	1	0	2	0	7	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.112	6	0	1	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.115	17	0	4	0	0	0	0	0	12	0	0	0	0	0	0	0	36	0	3	0	0	0	1
.118	0	0	0	0	18	0	0	0	141	0	1	0	0	0	1	0	11	0	2	0	3	0	1
.120	0	0	0	0	2	0	0	0	4	0	0	0	0	0	0	0	3	0	0	0	0	0	0
.122	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.124	0	0	0	0	3	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.126	0	0	0	0	4	0	0	0	18	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.128	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.132	0	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.134	0	0	0	0	10	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.136	0	0	0	0	3	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.138	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.140	0	0	0	0	3	0	0	0	18	0	0	0	0	0	0	0	0	2	0	0	0	0	2
.142	0	0	0	0	22	2	0	0	86	0	0	0	0	0	0	0	1	1	0	0	0	0	0
.144	0	0	0	0	15	0	0	0	147	0	0	1	0	0	0	0	0	0	0	0	0	0	1
.146	0	0	0	0	0	1	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.148	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.150	0	0	0	0	28	2	0	0	6	1	0	0	0	0	0	0	0	16	1	0	0	0	0
.152	0	0	0	0	9	1	0	0	5	0	2	0	0	0	0	0	0	0	0	0	0	0	0
.154	0	0	0	0	8	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.156	0	0	0	0	7	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0
.158	0	0	0	0	42	0	0	0	8	0	0	2	1	1	0	0	0	0	0	0	0	0	0
.160	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.162	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.164	0	0	0	0	24	1	0	0	15	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.184	0	0	0	0	31	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.186	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
.188	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.190	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
.192	0	0	0	0	14	1	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.194	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.196	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.198	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12.200	0	0	0	0	3	0	0	0	3	0	1	0	0	0	1	0	13	0	0	0	0	0	0
.203	1	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.206	4	0	1	0	0	0	0	0	15	1	0	0	0	0	0	0	1	0	0	0	0	0	0
.209	4	0	5	0	3	0	2	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0
.212	16	0	0	0	17	0	0	0	17	0	0	0	0	0	0	0	5	0	1	0	0	0	0
.215	7	0	2	0	16	0	2	0	27	0	0	0	0	1	0	2	12	0	1	0	0	0	1
.218	1	0	4	0	9	0	0	2	11	0	0	0	0	0	0	0	6	0	0	0	0	0	4
.221	2	0	3	0	15	0	4	9	16	0	0	0	0	0	0	0	0	0	1	0	0	0	0
.224	0	0	0	0	48	0	0	2	201	0	0	0	0	0	0	0	2	0	0	0	0	0	2
.227	1	0	0	0	8	0	0	5	81	1	0	0	0	1	1	0	1	0	0	0	0	0	1
.230	3	0	6	0	1	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.233	45	0	3	0	3	0	1	2	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	*Bathylagus nigrigenys*	*Leuroglossus stilbius urotranus*	*Nansenia* spp.	*Araiophos* sp.	*Cyclothone* spp.	*Diplophos* sp.	*Ichthyococcus* spp.	*Maurolicus muelleri*	*Vinciguerria* spp.	*Bathophilus filifer*	Evermannellidae	*Macroparalepis macrurus*	*Sudis atrox*	*Scopelo saurus* spp.	*Oxyporhamphus micropterus*	Trachypteridae	*Auxis* spp.	*Katsuwonis pelamis*	*Coryphaena* spp.	*Naucrates ductor*	*Howella pammelas*	*Tetragonurus* sp.	Ceratioidei
12.235	25	0	1	0	9	0	1	0	49	0	0	0	0	0	0	0	11	0	0	0	0	0	1
.238	17	0	0	0	7	0	1	0	31	3	0	1	0	0	0	0	17	0	0	0	0	0	0
.240	11	0	1	0	3	2	0	0	14	3	0	1	0	0	0	0	23	0	1	0	2	0	1
.242	1	0	2	0	1	0	0	0	0	7	0	0	0	0	2	0	12	0	1	0	3	0	0
.244	3	0	0	0	8	2	0	0	4	2	0	0	0	0	1	0	9	0	2	0	22	0	5
.246	11	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	8	0	1	0	7	0	2
.248	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	1	1	0	2	0	1	0	0
.250	1	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.252	1	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.254	1	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.256	3	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0
.258	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.260	2	0	0	0	4	1	0	0	15	0	0	0	0	0	0	0	0	0	0	0	2	0	2
.262	2	0	0	0	0	5	0	0	97	3	0	0	0	0	0	0	0	0	0	1	0	0	0
.264	2	0	0	0	0	6	0	0	14	1	0	0	0	0	0	0	0	0	0	1	0	0	0
.265	3	0	0	0	0	7	0	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.268	0	0	0	0	0	2	0	0	103	1	0	0	0	0	0	0	0	0	2	0	0	0	2
.270	1	0	0	0	0	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.272	4	0	0	0	0	5	0	0	38	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.274	0	0	0	0	0	4	0	0	36	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.276	0	0	0	0	0	0	0	0	138	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.278	1	0	0	0	0	1	0	0	164	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.280	0	0	0	0	2	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.282	1	0	0	0	0	2	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.284	0	0	0	0	1	1	0	0	118	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13.001	8	0	0	0	3	0	0	0	90	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.003	14	0	0	0	35	0	0	0	1130	1	1	2	0	0	0	0	0	0	0	0	1	0	0
.005	54	0	0	0	6	1	2	0	300	0	0	0	0	0	0	0	3	0	1	0	0	0	0
.007	9	0	0	0	2	0	0	0	11	0	0	0	0	0	0	0	7	0	0	0	0	0	1
.009	8	0	0	0	1	0	0	0	9	0	0	0	0	0	0	0	7	0	0	0	0	0	0
.011	6	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.013	18	0	0	0	0	0	1	0	8	0	0	0	0	0	1	0	1	0	0	0	0	0	0
.015	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
.017	16	0	0	0	1	0	1	0	61	1	0	0	0	0	0	1	8	0	1	0	0	0	0
.019	9	0	0	0	0	0	0	0	82	0	0	0	0	0	9	0	33	0	1	0	0	0	1
.021	4	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	20	0	0	0	0	0	0
.022	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.028	4	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.030	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	2
.032	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	52	0	0	0	0	0	8
.034	23	0	0	0	1	0	0	0	60	0	0	0	0	0	4	0	41	0	0	0	1	0	3
.036	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.038	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
.040	20	0	0	0	5	0	2	0	10	1	0	0	0	0	0	0	20	0	0	0	0	0	1
.042	11	0	0	0	5	0	3	0	6	0	0	0	0	0	0	1	4	0	0	0	0	0	0
.044	10	0	0	0	3	0	0	0	11	0	0	0	0	0	0	1	1	0	0	0	0	0	0
.046	10	0	0	0	5	0	0	0	73	4	0	0	0	0	0	1	0	0	1	0	0	0	0
.048	29	0	0	0	19	0	0	0	291	2	0	0	0	0	1	0	1	0	1	0	6	0	4
.050	10	0	0	0	5	0	0	0	36	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.052	13	0	0	0	16	0	1	1	181	0	0	4	0	0	0	0	0	0	1	0	5	0	0
.054	14	0	1	0	9	1	0	5	76	4	0	0	0	0	3	0	11	0	0	0	0	0	1
.056	33	0	1	0	29	0	2	27	454	16	1	1	0	0	0	0	0	0	0	0	6	0	0
.058	6	0	0	0	8	0	1	10	319	1	0	0	0	0	0	0	7	0	0	0	0	0	0

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia spp.	Araiophos sp.	Cyclothone spp.	Diplophos sp.	Ichthyococcus spp.	Maurolicus muelleri	Vinciguerria spp.	Bathophilus filifer	Evermannellidae	Macroparalepis macrurus	Sudis atrox	Scopelo saurus spp.	Oxyporhamphus micropterus	Trachypteridae	Auxis spp.	Katsuwonis pelamis	Coryphaena spp.	Naucrates ductor	Howella pammelas	Tetragonurus sp.	Ceratioidei
13.060	5	0	0	0	2	0	2	14	8	0	0	0	0	0	0	0	17	0	0	0	0	0	0
.062	7	0	0	0	0	0	0	3	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.064	15	0	0	0	5	0	3	18	45	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.065	2	0	0	0	4	0	1	11	56	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.067	7	0	0	0	2	0	0	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.069	37	0	1	0	2	0	0	13	45	1	0	0	0	0	0	0	1	0	0	0	0	0	0
.071	37	0	0	0	17	0	0	0	555	6	0	0	0	0	1	0	14	0	4	0	0	0	1
.073	42	0	0	0	13	0	0	0	153	1	0	0	0	0	0	0	3	0	4	0	0	0	5
.075	8	0	0	0	3	0	0	0	18	0	0	0	0	0	0	0	1	0	1	0	0	0	0
.077	0	0	0	0	0	0	0	0	59	2	0	0	0	0	0	0	5	0	0	0	0	0	2
.079	0	0	0	0	1	0	0	0	134	0	0	0	0	0	0	0	5	0	0	0	0	0	1
.081	2	0	0	0	0	0	0	0	164	0	0	1	0	0	0	0	0	0	0	0	0	0	1
.083	5	0	0	0	0	0	0	0	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.085	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.087	0	0	0	0	2	0	0	0	64	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.089	0	0	0	0	9	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.091	0	0	0	0	0	0	0	0	11	0	0	1	0	0	0	0	2	0	1	0	1	0	0
.093	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.095	6	0	0	0	25	1	0	0	120	2	1	1	0	0	0	0	10	0	0	0	0	0	1
.097	3	0	0	0	11	0	1	0	87	1	1	2	0	0	0	0	1	0	0	0	0	0	0
.099	0	0	0	0	4	1	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13.101	3	0	0	0	0	0	1	0	7	0	0	2	0	0	0	0	0	0	1	0	0	0	0
.103	1	0	0	0	36	0	0	0	125	1	2	2	0	0	0	0	0	0	0	0	0	0	6
.105	0	0	0	0	20	0	0	0	30	0	0	1	0	0	0	0	0	0	0	0	0	1	2
.107	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.109	0	0	0	0	1	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.111	0	0	0	0	7	0	0	0	11	0	0	0	0	1	0	0	0	0	0	0	0	0	0
.113	0	0	0	0	12	0	0	0	18	0	0	1	1	0	0	1	0	0	0	0	0	0	1
.115	0	0	0	0	4	0	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0
.117	0	0	0	0	4	1	0	0	4	1	0	0	1	0	0	0	0	0	0	0	0	1	0
.119	0	0	0	0	26	3	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.121	0	0	0	0	10	0	1	0	6	0	0	0	1	0	0	0	0	0	0	0	0	0	0
.123	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.125	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.127	0	0	0	0	13	0	0	0	7	0	0	0	1	0	0	0	0	0	0	0	0	0	0
.129	0	0	0	0	9	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.131	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.133	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.135	0	0	0	0	46	0	0	0	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0
.137	0	0	0	0	12	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.139	0	0	0	0	3	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.141	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.143	0	0	0	0	21	0	0	0	55	0	0	0	1	0	0	0	5	0	0	0	0	0	0
.145	0	0	0	0	12	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.147	0	0	0	0	1	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	3
.149	0	0	0	0	6	0	0	0	8	0	0	0	0	0	0	1	0	0	1	0	0	0	0
.151	0	0	0	0	7	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.153	0	0	0	0	44	0	0	0	59	0	3	0	0	0	0	0	0	0	0	0	0	0	0
.155	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.157	0	0	0	0	3	0	0	0	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.159	0	0	0	0	8	1	0	0	3	0	1	1	0	0	0	0	4	0	0	0	0	0	0
.161	0	0	0	0	11	0	0	0	13	0	0	1	0	0	0	0	0	0	0	0	0	0	0
.163	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.165	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia spp.	Araiophos sp.	Cyclothone spp.	Diplophos sp.	Ichthyococcus spp.	Maurolicus muelleri	Vinciguerria spp.	Bathophilus filifer	Evermannellidae	Macroparalepis macrurus	Sudis atrox	Scopelosaurus spp.	Oxyporhamphus micropterus	Trachypteridae	Auxis spp.	Katsuwonis pelamis	Coryphaena spp.	Naucrates ductor	Howella pammelas	Tetragonurus sp.	Ceratioidei
13.167	0	0	0	0	5	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.169	0	0	0	0	7	0	0	0	76	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.171	0	0	0	0	2	0	0	0	16	0	0	0	0	0	0	0	13	0	0	0	0	0	0
.173	7	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	6	0	0	0	0	0	0
.175	22	0	0	0	6	0	0	0	169	0	1	1	0	0	0	0	45	0	0	0	1	0	1
.179	15	0	0	0	6	0	0	0	105	0	0	0	0	0	1	0	7	0	0	0	0	0	1
.183	50	0	3	0	3	0	0	0	36	0	0	0	0	0	0	0	6	0	0	0	0	0	0
.187	43	0	2	0	3	0	0	0	26	0	0	0	0	0	0	0	0	0	1	0	0	0	0
.191	10	0	6	0	25	0	0	5	118	0	0	0	0	0	1	0	7	0	0	0	0	0	1
.195	10	0	0	0	8	0	0	0	194	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.199	5	0	0	0	1	0	0	2	25	0	0	0	0	0	0	0	0	0	0	0	0	0	1
13.203	3	0	1	0	2	0	0	9	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.207	11	0	0	0	11	0	0	7	143	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.211	5	0	0	0	6	0	2	1	27	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.215	6	0	0	0	3	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.219	9	0	0	0	1	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.223	2	0	0	0	3	0	0	2	15	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.227	9	0	0	0	14	0	0	4	20	0	0	0	0	0	3	0	1	0	0	0	0	0	0
.231	9	0	1	0	5	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.235	9	0	1	0	3	0	2	0	31	0	0	0	0	0	1	0	1	0	0	0	0	0	0
.237	6	0	0	0	12	0	2	0	33	0	0	1	0	0	0	0	7	0	1	1	0	0	0
.239	3	0	0	0	7	0	3	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.241	2	0	0	0	1	0	0	0	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.243	11	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.245	7	0	0	0	1	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.247	9	0	0	0	0	0	0	0	11	0	0	0	0	0	0	1	2	0	1	0	0	0	0
.249	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.251	6	0	0	0	0	0	0	0	10	2	0	0	0	0	0	0	3	0	0	0	0	0	0
.253	20	0	0	0	0	0	0	0	22	4	0	0	0	0	0	0	0	0	0	0	0	0	0
.255	7	0	0	0	0	0	0	0	29	0	0	0	0	0	1	0	15	0	1	0	0	0	3
.257	8	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0
.259	17	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	5	0	0	0	0	0	0
.261	8	0	0	0	1	0	0	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.263	19	0	0	0	0	0	0	0	54	0	0	0	0	0	1	0	11	0	0	0	0	0	0
.265	6	0	0	0	0	1	0	0	12	8	0	0	0	0	0	0	1	0	0	0	0	0	1
.266	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0
.268	3	0	0	0	0	0	0	0	26	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.270	4	0	0	0	0	2	0	0	18	3	0	0	0	0	12	0	1	0	0	0	0	0	1
.272	2	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0
.274	1	0	0	0	0	3	0	0	49	6	0	0	0	0	3	0	1	0	1	0	0	0	0
.276	5	0	0	0	0	2	0	0	89	3	0	0	0	0	3	0	19	0	0	0	0	0	0
.278	1	0	0	0	0	1	0	0	20	2	0	0	0	0	0	0	0	0	0	0	0	0	0
.280	8	0	0	0	0	3	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.282	0	0	0	0	0	3	0	0	33	6	0	0	0	0	1	0	0	0	1	0	0	0	0
.284	18	0	0	0	1	0	0	0	60	1	0	0	0	0	2	0	0	0	0	0	0	0	1
13.318	13	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
.320	8	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	13	0	0	0	0	0	0
.322	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	9	0	1	0	0	0	0
.324	10	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	4	0	0	0	0	0	0
.326	13	0	0	0	1	0	0	0	9	0	0	0	0	0	0	0	18	0	0	0	0	0	1
.328	2	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	7	0	0	0	0	0	0
.330	4	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.332	11	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	1

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	*Bathylagus nigrigenys*	*Leuroglossus stilbius urotranus*	*Nansenia* spp.	*Araiophos* sp.	*Cyclothone* spp.	*Diplophos* sp.	*Ichthyococcus* spp.	*Maurolicus muelleri*	*Vinciguerria* spp.	*Bathophilus filifer*	Evermannellidae	*Macroparalepis macrurus*	*Sudis atrox*	*Scopelosaurus* spp.	*Oxyporhamphus micropterus*	Trachypteridae	*Auxis* spp.	*Katsuwonis pelamis*	*Coryphaena* spp.	*Naucrates ductor*	*Howella pammelas*	*Tetragonurus* sp.	Ceratioidei
13.334	37	0	0	0	2	0	0	0	19	1	0	0	0	0	0	1	0	0	0	0	0	0	2
.338	9	0	1	0	1	0	0	0	48	0	0	0	0	0	2	0	5	0	0	0	0	0	0
.340	4	0	0	0	3	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	1	0	0
.342	9	0	1	0	8	0	0	2	14	0	0	0	0	0	0	0	4	0	0	0	0	0	0
14.001	9	30	0	0	3	0	0	0	94	0	0	0	0	0	0	0	8	0	0	0	0	0	0
.006	3	29	0	0	3	0	0	0	15	0	0	0	0	0	0	0	10	0	0	0	0	0	0
.008	9	25	1	0	0	0	0	0	4	0	0	0	0	0	0	0	1	0	1	0	0	0	1
.010	1	13	0	0	3	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.012	2	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.014	3	39	0	0	0	0	0	0	4	0	0	0	0	0	0	0	2	0	0	0	0	0	0
.016	10	9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
.017	11	6	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.018	24	17	0	0	6	0	0	0	42	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.020	6	0	0	0	0	0	0	0	10	0	0	0	0	0	0	1	0	0	0	0	0	0	0
.022	1	6	0	0	3	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.024	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.027	17	6	0	0	1	0	0	0	30	0	0	0	0	0	0	0	6	0	0	0	0	0	0
.029	13	11	0	0	1	0	0	0	41	0	0	0	0	0	0	0	0	0	2	0	0	0	2
.031	29	1	0	0	2	0	0	0	41	0	0	0	0	1	0	0	1	0	1	0	0	0	0
.033	20	1	0	0	0	0	1	0	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0
.040	48	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	6	0	2	0	0	0	0
.043	59	6	0	0	3	0	0	0	14	1	0	0	0	6	0	0	22	0	0	0	0	0	5
.047	49	62	0	0	0	0	0	1	2	0	0	0	0	0	2	0	9	0	1	1	0	0	0
.051	20	205	0	0	2	0	0	0	25	0	0	0	0	0	0	0	46	0	0	1	0	0	0
.055	2	152	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.060	0	139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.066	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.069	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.076	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.078	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.081	2	0	0	0	3	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.084	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.086	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.088	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.091	2	0	0	0	8	0	0	0	32	1	0	0	0	0	0	0	0	0	1	0	0	0	2
.095	2	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
.099	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14.103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.110	0	0	0	0	5	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0
.112	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.115	2	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.117	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.120	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.122	2	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.123	7	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.124	7	0	0	0	18	0	0	0	58	0	0	0	0	0	0	1	0	0	1	0	0	0	8
.126	3	0	0	0	3	0	1	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.127	5	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.128	5	0	0	0	4	0	0	0	56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.130	3	0	0	0	2	0	0	0	42	0	0	0	0	0	0	0	4	0	0	0	0	0	0

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC I.—*Continued.*

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia spp.	Araiophos sp.	Cyclothone spp.	Diplophos sp.	Ichthyococcus spp.	Maurolicus muelleri	Vinciguerria spp.	Bathophilus filifer	Evermannellidae	Macroparalepis macrurus	Sudis atrox	Scopelo saurus spp.	Oxyporhamphus micropterus	Trachypteridae	Auxis spp.	Katsuwonis pelamis	Coryphaena spp.	Naucrates ductor	Howella pammelas	Tetragonurus sp.	Ceratioidei
14.131	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.132	8	0	0	0	0	0	0	0	17	0	0	0	0	0	0	1	0	0	1	0	0	0	2
.134	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1
.136	1	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.138	9	0	0	0	2	0	0	0	90	0	0	0	0	0	0	0	9	0	0	0	0	0	0
.142	1	0	0	0	0	0	0	0	53	4	0	0	0	0	0	0	1	0	0	0	0	0	1
.146	16	30	0	0	0	0	0	0	111	1	0	0	0	0	0	0	8	0	0	0	0	0	0
.150	33	1	0	0	2	0	0	1	45	0	0	0	0	0	4	1	5	0	0	0	0	0	0
.154	28	6	0	0	9	0	1	0	372	0	0	0	0	0	1	0	7	0	0	0	0	0	3
.158	0	0	0	0	4	0	0	1	219	1	0	0	0	0	0	0	0	0	0	0	0	0	1
.164	8	0	0	0	4	0	1	0	48	0	0	0	0	3	0	0	6	0	0	0	0	0	1
.172	1	0	0	0	2	0	0	5	90	0	0	0	0	0	0	0	12	0	0	0	0	0	0
.174	3	0	0	0	0	0	1	3	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.177	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.183	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.188	34	0	0	0	4	0	0	9	155	1	0	0	0	0	2	0	36	0	1	0	0	0	1
.194	161	0	0	0	7	0	0	22	98	0	0	0	0	0	0	1	22	0	1	0	0	0	4
.195	54	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	2	0	0	0	0
.199	15	0	0	0	5	0	0	0	196	0	0	0	0	0	0	1	20	0	0	0	0	0	3
14.203	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1
.209	5	0	0	0	0	0	0	0	2	0	0	0	0	0	10	0	0	0	0	0	0	0	0
.213	34	0	0	0	10	0	0	0	86	0	0	0	0	0	0	0	11	0	1	0	0	0	0
.218	27	0	0	0	1	0	0	0	38	0	0	0	0	0	2	1	4	0	2	0	0	0	0
.220	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	13	0	0	0	0	0	0
.222	2	0	0	0	0	0	0	0	4	2	0	0	0	0	0	0	1	0	0	0	0	0	0
.224	9	3	0	0	6	0	0	0	31	1	0	0	0	0	0	0	7	0	0	0	1	0	0
.228	2	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	2	0	0	0	0	0	0
.230	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	9	0	0	0	0	0	0
.232	9	0	0	0	0	0	0	0	49	0	0	0	0	0	0	0	12	0	0	0	0	0	0
.234	9	0	0	0	2	0	0	0	867	0	0	0	0	0	0	1	161	1	0	0	0	0	0
.236	3	0	0	0	0	0	0	0	16	0	0	0	0	0	0	1	10	0	0	0	0	0	0
.240	21	0	0	0	0	1	0	4	31	0	0	0	0	0	0	0	85	0	0	0	0	0	1
.243	24	0	0	0	1	0	0	7	19	0	0	0	0	0	0	0	5	0	0	0	0	0	0
.247	4	0	0	0	0	0	0	13	39	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.251	8	3	0	0	1	0	0	1	23	0	0	0	0	0	0	0	1	0	0	0	0	0	6
.255	1	209	0	0	10	0	0	0	76	0	0	0	0	0	0	0	59	0	1	0	0	0	6
.259	16	0	0	0	0	0	0	0	40	1	0	0	0	0	0	0	0	0	0	0	0	0	5
.263	2	0	0	0	2	0	0	0	231	0	0	0	0	0	0	0	0	0	0	0	0	0	2
.267	3	0	0	0	0	0	0	0	33	0	0	0	0	0	0	1	0	0	2	0	0	0	3
.276	9	0	0	0	6	0	0	0	52	0	0	0	0	0	0	0	0	0	2	0	0	0	1
.280	7	0	0	0	3	0	0	0	59	2	0	0	0	0	0	0	0	0	2	0	0	0	6
.283	3	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	1	0	0	0	1
.287	5	0	0	0	3	0	0	0	59	0	0	0	0	0	0	0	0	0	0	0	0	0	9
.291	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.295	4	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	63	0	2	0	0	0	5
.300	1	286	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
.303	3	490	0	0	2	0	0	0	8	0	0	0	0	0	0	0	0	0	1	0	1	0	1
.306	12	22	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.310	70	21	0	0	0	0	0	9	12	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.314	24	0	0	0	1	0	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.318	32	0	0	0	2	0	0	2	66	0	0	0	0	0	0	0	1	0	0	0	0	0	1
.323	11	0	0	0	0	0	0	0	24	1	0	0	0	0	0	0	0	0	0	0	0	0	0
.326	15	12	0	0	1	0	0	0	65	0	0	0	0	0	0	0	8	0	0	0	0	0	0
.330	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix Table 4.—Summary of occurrences and numbers of larvae of eight families, limited in distribution to a broad coastal band or around offshore islands.

STATION NUMBER	Clupeidae	Engraulidae	Synodontidae	Carangidae	Serranidae	Labridae	Gobiidae	Scorpaenidae
11.076	0	0	0	1	0	0	0	0
11.246	0	0	0	0	0	0	0	1
12.020	0	0	0	0	0	1	0	0
.024	0	0	0	1	4	0	0	0
.026	0	0	0	0	10	0	0	0
.028	0	0	0	0	0	0	3	3
.030	0	0	0	0	0	0	1	1
.031	0	0	0	0	0	0	7	0
.033	1	2	1	2	1	2	1	1
.035	0	0	0	5	0	0	3	1
.041	0	0	0	1	0	0	1	0
.059	0	0	0	0	0	0	1	0
12.221	0	0	0	0	0	0	0	2
.256	0	0	0	0	0	1	0	0
.262	0	0	0	1	0	0	0	0
.264	0	0	0	1	0	0	0	0
.268	0	0	0	1	0	0	0	0
13.003	0	0	0	1	0	0	1	0
.005	0	0	0	0	0	0	1	1
.007	0	0	0	0	0	0	0	1
.011	0	0	0	0	0	0	1	0
.019	0	13	1	70	49	2	47	12
.021	2	7	0	11	3	0	3	1
.030	0	0	0	0	0	0	1	2
.032	0	0	0	0	0	0	12	8
.034	0	0	0	0	0	0	23	3
.040	0	0	0	0	0	0	0	1
.042	0	0	0	0	0	1	0	0
.054	0	0	0	0	1	0	0	0
.056	0	0	0	0	0	0	1	0
.062	0	0	0	0	0	2	0	0
13.235	0	0	0	0	0	0	0	1
.237	0	0	0	1	0	0	0	0
.239	0	0	0	0	0	0	2	0
.245	0	0	0	0	0	0	13	0
.247	0	0	0	0	0	0	5	0
.249	0	0	0	0	0	0	1	0
.253	0	0	0	0	0	0	72	0
.255	2	0	1	2	0	0	2	3
.257	0	0	0	0	0	0	0	1
.261	0	0	0	0	0	0	41	0
.263	0	0	0	0	0	0	0	2
.265	0	0	0	0	0	0	0	1
.266	0	0	0	0	0	1	0	0
.268	0	0	0	0	0	1	0	0
.274	0	0	0	0	0	0	3	0
.276	0	0	0	0	0	0	2	0
13.320	1	0	0	0	0	1	7	3
.328	0	0	0	0	0	0	2	1
.330	0	0	0	0	0	0	4	0
.334	0	0	0	0	0	0	1	0
.338	0	0	0	0	0	0	17	0
14.001	0	5	1	1	84	0	55	11
.006	0	0	0	0	1	0	5	1
.008	0	0	0	0	0	0	2	5
.010	0	0	0	0	0	0	3	2
.012	0	0	1	0	0	1	1	0
.014	6	0	0	4	0	0	11	1
.016	0	0	0	34	0	0	0	0
.017	0	0	0	0	0	1	0	0
.018	0	0	0	0	0	3	10	4
.020	0	0	0	0	0	1	1	1
.022	0	0	0	0	14	0	2	1
.024	0	4	0	6	5	0	0	6
.027	0	0	3	5	1	4	36	9
.029	0	0	7	2	12	0	9	37
.031	0	0	3	0	3	1	18	4
.033	0	0	0	1	0	1	1	2
.040	0	0	0	6	5	0	1	0
.043	0	0	0	0	0	1	2	0
.047	0	0	0	1	0	1	0	3
.051	0	0	0	1	0	0	0	6
.055	0	0	0	0	0	1	0	0
.060	0	52	0	2	0	0	0	0
.066	0	11	0	0	0	0	0	0
.069	0	97	0	0	0	0	0	0
.076	0	11	0	0	0	0	0	0
14.106	0	3	0	0	0	0	0	0
.110	0	0	0	1	0	0	0	0
.154	0	0	0	0	5	0	0	1
.158	5	0	0	1	8	0	3	4
.164	0	0	0	0	0	0	0	1
.172	2	0	0	11	22	3	0	1
.174	1	0	0	0	4	2	1	1
.177	60	0	0	2	6	1	1	0
.194	1	0	0	1	0	1	0	0
.195	0	0	0	0	2	0	0	0
.199	0	0	0	2	0	0	1	0
14.209	0	0	0	0	0	1	0	0
.213	0	0	0	0	0	0	3	0
.220	0	0	0	0	0	1	1	0
.222	0	0	0	0	0	1	0	0
.224	0	0	0	3	0	0	0	1
.228	0	0	0	0	1	0	0	4
.230	0	0	0	2	0	0	0	2
.232	0	0	0	0	0	0	2	0
.234	0	0	0	0	3	0	8	3
.236	0	0	0	0	0	0	1	0
.240	0	0	0	0	0	0	1	1
.243	0	0	0	0	0	0	1	0
.247	0	0	0	0	0	0	2	0
14.303	0	0	0	0	1	1	0	0
.314	0	0	0	0	0	0	0	1
.318	0	0	10	0	4	2	43	5
.323	0	0	0	0	1	0	3	1
.326	0	0	13	0	2	0	23	0

Appendix Table 5.—Numbers and kinds of larvae of Gempylidae-Trichiuridae obtained in EASTROPAC I collections.

STATION NUMBER	Nealotus tripes	Gempylus serpens	Diplospinus multistriatus	Lepidopus sp.	Other
11.056	0	1	0	0	0
.064	0	0	1	0	0
.072	0	1	0	0	0
11.114	1	0	0	0	0
.138	1	0	0	0	0
.140	1	0	0	0	0
.146	0	1	0	0	0
.158	1	0	0	0	0
.159	1	0	0	0	0
11.213	0	1	0	0	0
.219	0	1	0	0	0
.228	1	0	0	0	0
.234	0	1	0	0	0
.295	0	2	0	0	0
.297	0	2	0	0	0
11.318	0	0	5	0	0
.320	0	0	1	0	0
.324	0	0	1	0	0
.326	0	0	2	0	0
12.004	0	1	0	0	0
.014	0	1	0	0	0
.020	0	1	0	0	0
.047	0	2	0	0	0
.081	0	1	0	0	0
12.115	0	0	0	0	1
.118	6	0	0	0	1
.120	1	0	0	0	0
.144	0	1	0	0	0
.150	0	3	0	0	0
.152	0	1	0	0	0
.158	0	1	0	0	0
.188	0	1	0	0	0
12.246	0	2	0	0	0
.260	0	1	0	0	0
.262	0	1	0	0	0
.272	0	1	0	0	0
.276	0	1	0	0	0
13.048	1	2	0	0	0
.054	0	0	0	17	0
.056	2	0	0	0	0
.071	6	0	0	0	0
.073	7	0	0	0	0
.075	2	0	0	0	0
.077	3	0	0	0	0
.081	8	0	0	0	0
.083	0	1	0	0	0
.095	0	0	7	0	0
.097	0	1	4	0	0
.101	0	1	6	0	0
.103	0	0	7	0	0
.105	0	0	2	0	0
13.107	0	0	1	0	0
.119	1	3	0	0	0
.137	0	2	0	0	0
.139	0	0	1	0	0
.147	0	0	1	0	0
.153	0	0	1	0	0
.159	0	2	0	0	0
.167	1	0	0	0	0
.171	0	1	0	0	0
.173	1	0	0	0	0
.175	1	0	0	0	0
.179	0	3	0	0	0
.187	0	0	0	0	2
.191	0	1	0	0	0
13.235	1	0	0	0	0
.245	0	1	0	0	0
.280	0	0	0	0	1
14.001	0	1	0	0	0
.010	1	0	0	0	0
.012	0	0	0	1	0
.029	1	0	1	1	0
.031	1	0	0	0	0
.095	0	0	1	0	0
14.122	0	0	1	0	0
.123	0	0	1	0	0
.124	1	1	1	0	0
.126	1	0	1	0	0
.127	0	0	3	0	0
.128	0	0	6	0	0
.130	0	0	3	0	0
.131	0	0	1	0	0
.134	1	1	0	0	0
.138	3	0	0	0	0
.142	2	0	0	0	0
.146	2	0	0	0	0
.150	1	0	0	0	0
.164	1	0	0	0	0
.188	1	0	0	0	0
.194	0	0	0	2	0
.195	1	0	0	0	0
14.222	1	0	0	0	0
.224	1	0	0	0	0
.234	8	0	0	1	0
.240	1	0	0	0	0
.259	3	0	0	0	0
.280	1	4	1	0	0
.283	0	0	1	0	0
.287	1	2	0	0	0
.295	0	1	0	0	0
14.318	1	0	0	2	0
.326	0	0	0	1	0
.330	1	0	0	0	0

APPENDIX TABLE 6.—Numbers and kinds of flatfish (Pleuronectiformes) larvae obtained in EASTROPAC I collections.

Station number	*Bothus leopardinus*	*Citharichthus* - *Etropus*	*Cyclopsetta* sp.	*Engyophrys sancti-laurentii*	*Syacium ovale*	*Symphurus* spp.	Other Pleuronectiformes
12.028	0	0	0	0	0	1	0
.030	0	1	0	0	0	0	0
.031	0	0	0	0	2	6	0
.033	4	1	0	0	6	6	0
.035	0	0	0	0	0	3	0
.045	0	0	0	0	0	1	0
13.007	0	0	0	0	1	0	0
.009	0	1	0	0	0	0	0
.011	0	1	0	0	0	0	0
.013	0	0	0	0	0	5	0
.015	1	0	0	0	0	1	0
.019	6	1	1	0	25	31	1
.021	2	2	0	0	13	8	0
.030	0	0	0	0	0	4	0
.032	0	0	0	0	0	8	0
.034	0	0	0	2	4	9	0
.036	0	0	0	0	1	0	0
.040	1	2	0	1	0	3	0
.042	1	0	1	0	6	1	0
.054	1	0	0	0	0	0	0
13.245	1	0	0	0	0	0	0
.251	0	0	0	0	0	1	0
.253	4	0	0	0	0	4	0
.255	3	1	0	0	0	9	0
.257	0	0	0	0	0	1	0
.259	0	0	0	0	1	1	0
.261	1	0	0	0	1	1	0
.263	1	0	0	0	3	8	0
.265	0	0	0	0	2	1	0
13.318	2	0	0	0	1	1	0
.320	2	0	0	0	0	2	0
.322	5	0	0	0	0	0	0
.324	0	0	0	0	1	0	0
.326	0	0	0	0	1	2	0
.328	0	0	0	0	0	1	0
.334	1	0	0	0	0	0	0
14.001	1	5	0	1	0	35	0
.006	0	1	0	0	0	2	0
.008	0	1	0	0	0	3	0
.010	0	1	0	1	0	1	0
.014	0	2	0	0	0	4	0
.016	0	0	0	0	0	5	1
.017	0	0	0	0	0	2	0
.018	0	1	0	0	0	1	0
.020	0	0	0	0	0	5	0
.022	1	3	0	0	0	1	0
.024	0	1	0	0	0	9	0
.027	1	6	0	1	3	9	0
.029	1	5	0	0	2	24	0
.031	0	0	0	1	0	30	0
.033	0	0	0	1	0	2	0
.040	0	1	0	0	2	4	0
.047	0	0	0	0	0	1	0
.055	0	1	0	0	0	2	0
14.164	1	0	0	0	0	1	0
.174	0	0	0	0	0	1	0
.183	0	0	0	0	0	1	0
.194	0	0	0	0	0	1	0
.195	0	0	0	0	0	1	0
.199	0	0	0	0	0	1	0
14.209	0	0	0	0	0	1	0
.213	0	0	0	0	1	0	0
.220	0	0	0	0	0	3	0
.228	0	1	0	0	0	3	0
.230	0	0	0	0	0	1	0
.232	0	0	0	0	1	0	0
.234	2	0	2	0	3	1	0
.236	1	0	0	0	0	2	0
.240	0	0	0	0	1	0	0
.259	2	0	0	0	0	0	0
.295	0	1	0	0	0	0	0
14.300	0	0	0	0	1	0	0
.303	1	1	0	0	0	1	0
.306	0	0	0	0	0	1	0
.314	0	0	0	0	0	1	0
.318	1	2	0	1	0	19	0
.323	1	3	0	0	2	2	0
.326	1	4	0	0	0	3	0
.330	0	0	0	0	0	1	0

APPENDIX TABLE 7.—Standardized haul factors (SHF): These factors are used to adjust original counts of larvae to the comparable standard of numbers of larvae in 10 m³ of water strained per meter of depth fished.

Station	SHF	Station	SHF	Station	SHF	Station	SHF	Station	SHF
11.022	3.06	11.156	2.74	11.291	3.46	12.061	3.33	12.192	3.27
11.025	2.87	11.158	3.12	11.293	2.93	12.063	3.27	12.194	3.45
11.027	2.38	11.159	2.64	11.295	3.16	12.065	3.23	12.196	3.32
11.030	2.47	11.161	3.35	11.297	2.86	12.067	3.36	12.198	3.40
11.032	3.01	11.163	2.64	11.299	3.57	12.068	3.39	12.200	3.18
11.034	3.64	11.167	2.97	11.301	3.31	12.071	3.34	12.203	3.29
11.036	3.04	11.169	3.27	11.303	3.19	12.075	3.33	12.206	3.53
11.038	2.80	11.171	2.92	11.306	3.22	12.077	3.42	12.209	3.51
11.040	3.32	11.173	2.94	11.308	3.15	12.079	3.56	12.212	3.32
11.044	2.81	11.175	3.47	11.310	3.19	12.091	3.53	12.215	3.27
11.046	3.24	11.177	1.36	11.312	3.42	12.084	3.73	12.218	3.02
11.048	3.08	11.179	3.37	11.314	3.18	12.087	3.86	12.221	3.07
11.050	2.36	11.181	2.74	11.316	2.84	12.090	3.10	12.224	2.58
11.052	2.86	11.183	2.92	11.318	3.27	12.092	2.55	12.227	2.96
11.054	2.54	11.185	3.19	11.320	3.34	12.094	2.29	12.230	3.72
11.056	2.90	11.187	2.75	11.322	3.01	12.097	3.01	12.233	2.66
11.058	3.28	11.189	3.00	11.324	3.02	12.100	2.48	12.235	3.56
11.060	3.15	11.191	3.79	11.326	2.84	12.103	3.28	12.238	3.21
11.062	3.72	11.195	3.11	11.328	2.62	12.106	3.55	12.240	3.22
11.064	3.01	11.197	3.14			12.109	3.39	12.242	3.41
11.066	2.12	11.199	2.46	12.002	3.12	12.112	3.43	12.244	3.36
11.068	2.62	11.201	3.27	12.004	3.02	12.115	3.48	12.246	3.14
11.070	2.25	11.203	3.09	12.006	3.31	12.118	2.45	12.248	3.07
11.072	3.43	11.205	3.20	12.008	3.08	12.120	3.46	12.250	2.49
11.076	2.92	11.207	3.65	12.010	3.13	12.122	3.43	12.252	2.33
11.080	2.45	11.209	3.06	12.012	3.17	12.124	3.17	12.254	3.30
11.084	2.70	11.211	3.39	12.014	3.28	12.126	3.47	12.256	3.26
11.088	3.19	11.213	2.87	12.016	3.17	12.128	3.30	12.258	3.26
11.094	3.61	11.215	3.13	12.018	3.13	12.130	3.35	12.260	3.51
11.098	1.78	11.217	2.90	12.020	3.12	12.132	3.38	12.262	2.98
11.102	2.72	11.219	3.36	12.022	3.43	12.134	3.29	12.264	3.38
11.106	1.36	11.221	2.92	12.024	3.11	12.136	3.22	12.265	3.27
11.110	2.95	11.223	3.71	12.026	3.30	12.138	3.38	12.268	3.35
11.114	3.35	11.226	3.05	12.028	3.44	12.140	3.00	12.270	3.36
11.118	4.65	11.228	3.29	12.030	3.44	12.142	3.42	12.272	3.12
11.120	3.68	11.234	3.65	12.032	3.32	12.144	3.20	12.274	3.28
11.124	3.67	11.238	3.41	12.033	3.21	12.146	4.36	12.276	3.34
11.128	2.85	11.242	3.77	12.035	3.35	12.148	3.21	12.278	3.00
11.130	3.80	11.246	3.01	12.037	3.20	12.150	3.14	12.280	3.39
11.132	3.37	11.250	2.77	12.039	3.47	12.152	3.17	12.282	3.58
11.134	3.22	11.254	2.51	12.041	3.42	12.154	3.27	12.284	3.41
11.136	3.24	11.258	2.86	12.043	3.33	12.156	3.28		
11.138	3.38	11.262	3.23	12.045	3.35	12.158	3.22	13.001	2.26
11.140	2.77	11.266	2.91	12.047	3.42	12.160	3.49	13.003	2.45
11.142	3.35	11.270	3.69	12.049	3.39	12.162	3.21	13.005	1.42
11.146	3.25	11.278	3.09	12.051	3.31	12.164	2.98	13.007	2.42
11.148	2.54	11.282	3.99	12.053	3.27	12.184	3.22	13.009	2.56
11.150	3.45	11.285	3.20	12.055	2.84	12.186	3.22	13.011	3.68
11.152	2.59	11.287	3.45	12.057	3.22	12.188	3.35	13.013	2.29
11.154	3.40	11.289	3.12	12.059	3.41	12.190	3.39	13.015	2.76

APPENDIX TABLE 7.—Standardized haul factors (SHF): These factors are used to adjust original counts of larvae to the comparable standard of numbers of larve in 10 m^3 of water strained per meter of depth fished.—*Continued.*

Station	SHF	Station	SHF	Station	SHF	Station	SHF	Station	SHF
13.017	2.16	13.119	2.67	13.249	3.46	14.047	4.10	14.203	3.15
13.019	1.88	13.121	3.14	13.251	3.46	14.051	2.93	14.209	3.23
13.021	2.12	13.123	3.06	13.253	3.13	14.055	3.77	14.213	3.26
13.022	2.72	13.125	3.50	13.255	3.58	14.060	3.58	14.218	2.87
13.028	1.53	13.127	3.30	13.257	3.68	14.066	3.81	14.220	3.42
13.030	2.50	13.129	4.01	13.259	3.42	14.069	3.65	14.222	3.64
13.032	3.05	13.131	3.64	13.261	1.85	14.076	3.61	14.224	3.77
13.034	3.21	13.133	3.84	13.263	3.49	14.078	3.64	14.228	3.87
13.036	2.34	13.135	2.51	13.265	3.29	14.081	3.39	14.230	2.96
13.038	2.25	13.137	2.58	13.266	3.31	14.084	3.86	14.232	2.70
13.040	2.85	13.139	3.57	13.268	3.47	14.086	3.95	14.234	0.72
13.042	2.74	13.141	3.36	13.270	3.30	14.088	3.54	14.236	2.96
13.044	2.58	13.143	3.23	13.272	3.06	14.091	3.08	14.240	3.43
13.046	3.08	13.145	3.49	13.274	3.73	14.095	3.87	14.243	3.55
13.048	2.71	13.147	3.58	13.276	3.54	14.099	3.70	14.247	3.52
13.050	3.02	13.149	3.56	13.278	3.16	14.103	3.57	14.251	3.49
13.052	2.91	13.151	3.11	13.280	3.48	14.106	3.68	14.255	3.64
13.054	3.07	13.153	3.25	13.282	3.37	14.110	3.55	14.259	3.54
13.056	2.87	13.155	3.34	13.284	3.36	14.112	3.66	14.263	3.68
13.058	2.75	13.157	3.40	13.318	3.17	14.114	4.84	14.267	3.04
13.060	3.62	13.159	3.00	13.320	2.93	14.115	3.24	14.276	3.47
13.062	3.15	13.161	3.30	13.322	3.22	14.117	4.29	14.280	3.56
13.064	2.76	13.163	2.70	13.324	3.12	14.118	4.03	14.283	3.60
13.065	2.81	13.165	3.22	13.326	3.05	14.120	3.76	14.287	3.53
13.067	2.67	13.167	3.64	13.328	3.15	14.122	3.78	14.291	3.11
13.069	2.12	13.169	3.25	13.330	3.03	14.123	3.51	14.295	2.28
13.071	2.61	13.171	3.12	13.332	3.13	14.124	3.38	14.300	3.58
13.073	3.11	13.173	2.80	13.334	2.85	14.126	3.69	14.303	3.48
13.075	3.42	13.175	2.71	13.338	3.02	14.127	3.89	14.306	3.29
13.077	2.72	13.179	2.46	13.340	3.00	14.128	3.66	14.310	2.85
13.079	2.53	13.183	3.39	13.342	3.03	14.130	3.62	14.314	3.60
13.081	2.75	13.187	3.31			14.131	3.56	14.318	3.51
13.083	3.06	13.191	3.53	14.001	0.99	14.132	3.56	14.323	3.15
13.085	4.11	13.195	3.02	14.006	2.94	14.134	3.67	14.326	1.51
13.087	2.87	13.199	2.77	14.008	3.56	14.136	3.47	14.330	3.49
13.089	2.65	13.203	2.60	14.010	5.83	14.138	3.83		
13.091	2.97	13.207	3.31	14.012	3.50	14.142	3.69		
13.093	2.87	13.211	3.01	14.014	3.51	14.146	3.75		
13.095	2.81	13.215	2.97	14.016	3.28	14.150	3.60		
13.097	3.02	13.219	2.44	14.017	4.19	14.154	4.24		
13.099	2.64	13.223	3.01	14.018	3.13	14.158	2.45		
13.101	2.75	13.227	3.32	14.020	2.89	14.164	1.01		
13.103	2.77	13.231	2.42	14.022	3.45	14.172	3.55		
13.105	2.77	13.235	3.05	14.024	3.55	14.174	3.57		
13.107	2.76	13.237	3.56	14.027	3.55	14.177	3.88		
13.109	2.90	13.239	3.51	14.029	2.63	14.183	3.94		
13.111	2.88	13.241	3.55	14.031	2.03	14.188	2.15		
13.113	2.85	13.243	3.42	14.033	5.05	14.194	1.57		
13.115	3.46	13.245	2.98	14.040	3.65	14.195	1.39		
13.117	2.99	13.247	3.27	14.043	3.53	14.199	1.54		

7102

Management of the Pacific Sardine

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In 1967, the California Legislature placed a moratorium on landings of Pacific sardine *(Sardinops caerulea)* for any purpose, including bait. This was the most decisive act of management during the 50-year history of the fishery. It also was tacit admission that a viable fishery for the Pacific sardine had ceased to exist. A modest fishery for this species does continue off Baja California.

The history of the sardine fishery during the past 5 decades is best documented by the landings (Table 1). The fishery first developed in California and British Columbia, hence from its inception it was international. The tardiness of Oregon and Washington in entering the fishery was due to legal restrictions, not removed until 1935, against reduction of sardines to meal and oil. The fishery for the Pacific sardine grew rapidly during the first 2 decades, reached its highest level in the 1936-1937 season, continued at a high level for almost a decade, and then progressively declined. The decline was first evident in the Pacific Northwest; it progressed southward to central California and later to southern California. Even the catch off Ensenada, Baja California, has markedly declined in recent years, and most catches now are made from off central and southern Baja California.

Two principal uses were made of sardines: they were either canned or reduced to fish meal and oil. Most fish landed in British Columbia were reduced to fish meal and oil. The modest fisheries that developed in Oregon and Washington also were exclusively for reduction. California processors began as canners, and canning continued as an essential part of their operation, but they soon realized that reduction of whole fish to meal and oil could be a profitable supplement to the canning operation. The resulting controversy that developed between processors and management agencies is the main topic of discussion in this paper. Most Baja California landings have been canned.

The term "management" of a fishery has two entirely different meanings. Fishery scientists are striving for scientific management, designed to ensure a continuing high yield of the resource. This concept is often simplified to the phrase "maximum sustainable yield." Recently, many fishery scientists have redefined their goal to be an attempt to obtain the maximum economic yield for a fishery. Mostly, these attitudes remain concepts,

Table 1.—Seasonal catch (tons) of sardines along the Pacific coast [Each season includes June through the following May[1]]

					California[2]							
	Pacific Northwest				Northern California							
Season	British Columbia	Washington	Oregon	TOTAL	Reduction ships	San Francisco	Monterey	Total	Southern California	TOTAL California	Baja[3] California	Grand total
1916-17	. . .	. . .	. . .	. . .	. . .	. . .	7,710	7,710	19,820	27,530	. . .	27,530
1917-18	80	. . .	. . .	80	. . .	70	23,810	23,880	48,700	72,580	. . .	72,660
1918-19	3,640	. . .	. . .	3,640	. . .	450	35,750	36,200	39,340	75,540	. . .	79,180
1919-20	3,280	. . .	. . .	3,280	. . .	1,000	43,040	44,040	22,990	67,030	. . .	70,310
1920-21	4,400	. . .	. . .	4,400	. . .	230	24,960	25,190	13,260	38,450	. . .	42,850
1921-22	990	. . .	. . .	990	. . .	80	16,290	16,370	20,130	36,500	. . .	37,490
1922-23	1,020	. . .	. . .	1,020	. . .	110	29,210	29,320	35,790	65,110	. . .	66,130
1923-24	970	. . .	. . .	970	. . .	190	45,920	46,110	37,820	83,930	. . .	84,900
1924-25	1,370	. . .	. . .	1,370	. . .	560	67,310	67,870	105,150	173,020	. . .	174,390
1925-26	15,950	. . .	. . .	15,950	. . .	560	69,010	69,570	67,700	137,270	. . .	153,220
1926-27	48,500	. . .	. . .	48,500	. . .	3,520	81,860	85,380	66,830	152,210	. . .	200,710
1927-28	68,430	. . .	. . .	68,430	. . .	16,690	98,020	114,710	72,550	187,260	. . .	255,690
1928-29	80,510	. . .	. . .	80,510	. . .	13,520	120,290	133,810	120,670	254,480	. . .	334,990
1929-30	86,340	. . .	. . .	86,340	. . .	21,960	160,050	182,010	143,160	325,170	. . .	411,510
1930-31	75,070	. . .	. . .	75,070	10,960	25,970	109,620	146,550	38,570	185,120	. . .	260,190
1931-32	73,600	. . .	. . .	73,600	31,040	21,607	69,078	121,725	42,920	164,645	. . .	238,245
1932-33	44,350	. . .	. . .	44,350	58,790	18,634	89,599	167,023	83,667	250,690	. . .	295,040
1933-34	4,050	. . .	. . .	4,050	67,820	36,336	152,480	256,636	126,793	383,429	. . .	387,479
1934-35	43,000	. . .	. . .	43,000	112,040	68,477	230,854	411,371	183,683	595,054	. . .	638-054
1935-36	45,320	10	26,230	71,560	150,830	76,147	184,470	411,447	149,051	560,498	. . .	632,058
1936-37	44,450	6,560	14,200	65,210	235,610	141,099	206,706	583,415	142,709	726,124	. . .	791,334
1937-38	48,080	17,100	16,660	81,840	67,580	133,718	104,936	306,234	110,330	416,564	. . .	498,404
1938-39	51,770	26,480	17,020	95,270	43,890	201,200	180,994	426,084	149,203	575,287	. . .	670,557
1939-40	5,520	17,760	22,330	45,610	. . .	212,453	227,874	440,327	96,939	537,266	. . .	582,876
1940-41	28,770	810	3,160	32,740	. . .	118,092	165,698	283,790	176,794	460,584	. . .	493,324
1941-42	60,050	17,100	15,850	93,000	. . .	186,589	250,287	436,876	150,497	587,373	. . .	680,373
1942 43	65,880	580	1,950	68,410	. . .	115,884	184,399	300,283	204,378	504,661	. . .	573,071
1943-44	88,740	10,440	1,820	101,000	. . .	126,512	213,616	340,128	138,001	478,129	. . .	579,129
1944-45	59,120	20	. . .	59,140	. . .	136,598	237,246	373,844	181,061	554,905	. . .	614,045
1945-46	34,300	2,310	90	36,700	. . .	84,103	145,519	229,622	174,061	403,683	. . .	440,383

1946-47	3,990	6,140	3,960	14,090	...	2,869	31,391	34,260	199,542	233,802	...	247,892
1947-48	490	1,360	6,930	8,780	...	94	17,630	17,724	103,617	121,341	...	130,121
1948-49	...	50	5,320	5,370	...	112	47,862	47,974	135,752	183,726	...	189,096
1949-50	...	...	...	...	...	17,442	131,769	149,211	189,714	338,925	...	338,925
1950-51	...	...	...	...	...	12,727	33,699	46,426	306,662	353,088	...	353,088
1951-52	...	...	...	...	...	82	15,897	15,979	113,125	129,104	16,184	145,288
1952-53	...	...	...	...	...	...	49	49	5,662	5,711	9,162	14,873
1953-54	...	...	...	...	...	...	58	58	4,434	4,492	14,306	18,798
1954-55	...	...	...	...	...	...	856	856	67,609	68,465	12,440	80,905
1955-56	...	...	...	...	...	...	518	518	73,943	74,461	4,207	78,668
1956-57	...	...	...	...	...	...	63	63	33,580	33,643	13,655	47,298
1957-58	...	...	...	...	...	...	17	17	22,255	22,272	9,924	32,196
1958-59	...	...	...	...	...	...	24,701	24,701	79,270	103,971	22,334	126,305
1959-60	...	...	...	...	...	...	16,109	16,109	21,147	37,256	21,446	58,702
1960-61	...	...	...	...	...	...	2,340	2,340	26,538	28,878	19,899	48,777
1961-62	...	...	...	...	...	...	2,231	2,231	23,297	25,528	21,270	46,798
1962-63	...	...	...	...	...	...	1,211	1,211	2,961	4,172	14,620	18,792
1963-64	...	...	...	...	...	...	1,015	1,015	1,927	2,942	18,384	21,326
1964-65	...	...	...	...	...	...	308	308	5,795	6,103	27,120	33,223
1965-66	...	...	...	...	...	...	151	151	568	719	22,247	22,966
1966-67	...	...	...	...	...	...	23	23	321	344	19,531	19,875
1967-68[4]	...	...	...	...	...	...	10	10	61	71	27,657	27,728

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[1] Data for British Columbia were supplied by the Canadian Bureau of Statistics and the province of British Columbia; those for Washington by the Washington Department of Fisheries, and for Oregon by the Fish Commission of Oregon. Tonnages delivered to the reduction ships and data for Baja California were compiled by the United States Fish and Wildlife Service from the books of the companies receiving fish. California landings were derived from the records of the California Department of Fish and Game.

[2] Before the 1931-32 season, fish landed in Santa Barbara and San Luis Obispo Counties are included in Southern California. Beginning with the 1931-32 season fish landed north of Point Arguello are included in the Monterey landings and those south of Point Arguello are included in the Southern California landings.

[3] The amount of sardines landed in Baja California before the 1951-52 season is not known. Landings for Isla Margarita in Southern Baja California are not included since the landing data are incomplete. The partial record for this port indicated landings of 895 tons during the September 1965–May 1966 period and 203 tons during the June 1966–December 1966 period.

[4] Preliminary figures, estimated from percentage of sardines contained in loads of mixed fish as reported on California landing receipts. Under the moratorium on sardine landings a tolerance of up to 15% sardines was allowed in loads of mixed fish. In addition, an unknown amount of sardines (probably less than 500 tons) was landed illegally in 1967-68.

inasmuch as opportunities to apply scientific management to a resource have been exceedingly few; Pacific halibut and yellowfin tuna of the eastern Pacific are two notable exceptions.

Most management measures consist of piecemeal, pragmatic regulations, often influenced by special interest groups. These regulations are proclaimed by a federal agency for a territory, negotiated *quid pro quo* between nations, or passed by state legislatures and delegated to conservation agencies for implementation. The latter has been the usual pattern of managing the sardine resource.

The legal regulation of the sardine industry between 1917 and 1942 was summarized by Schaefer, Sette, and Marr (1951). In British Columbia no limitation was placed on the quantity of fish that could be used for reduction, but minor regulations were placed on fishermen as regards size and mesh of purse seine gear and, from time to time, on the season of fishing. Oregon and Washington, after approving the use of sardines for reduction, imposed no limitations on quantity landed or on season of fishing. Essentially, the fishery in the Pacific Northwest was a seasonal, opportunistic one, without regulation as to the quantity of landings or the use made thereof. The fishery off Baja California has had no legal restrictions on gear, seasons, quantities, or use.

Canning versus Reduction

Most of the legal regulation was in California and concerned the use of whole fish for reduction to fish meal and oil. To understand the controversy, a short historical account of the sardine processing industry in California is needed. Sardine canning began on a small scale as early as 1889 at San Francisco and 1894 at San Pedro. The industry grew slowly during the next 2 decades, although canneries were built at two additional ports, Monterey (1902) and San Diego (1909). The stimulus for greatly increasing the sardine pack came from food shortages during World War I. The case pack of sardines rose from less than 100,000 cases annually in 1915 to nearly 1 million cases in 1919. Monterey developed into the principal sardine canning port. San Pedro was a strong second, and activity was less in the San Francisco Bay area and at San Diego.

The sardine canning industry used mostly adult fish. Preparatory to canning, about 1/2 the weight of each fish was removed as waste material or offal, including the head, viscera, and usually a portion of the tail end. The cleaned fish were then packed, 4 to 8 per can, usually in tomato sauce or mustard, in the familiar 1-pound oval tins. These cans usually were packaged 48 per case which became the standard case pack of sardines. In the early days of the industry, the offal was barged to sea and discarded. During World War I, reduction plants were established at the principal ports to handle offal of canneries and surplus whole fish. These community reduction plants proved profitable, and for this reason short-lived; each cannery soon obtained its own reduction equipment. By 1920, most California sardine canneries had reduction facilities as part of their operation.

Processors soon learned that it was more profitable to convert sardines into meal and oil than to can them. Reduction of some whole fish was, at times, inevitable as part of the canning operation, inasmuch as wide fluctuations in landings of sardines sometimes created an oversupply. In addition, unavoidable machinery breakdowns at the canneries sometimes made it necessary to divert the sardines on hand to the reduction plant to avoid waste. Plant operators not only wished to increase the "overage" resulting from the canning operations, but to be permitted to reduce whole fish without regard to canning. Opposed to this unrestricted reduction was the sentiment of conservation organizations in California, succinctly stated in 1927 by B. D. Max Greene, attorney for the California Fish and Game Commission: "It seems repugnant to every right-thinking citizen to see fresh fish used for any purpose other than human consumption." These opposing interests—plant operators trying to gain permission to use as much of the sardine catch for reduction as they saw fit and conservation organizations seeking to curtail reduction—became the protagonists in a continuing struggle.

The first clash came as early as 1919. In the spring of that year, several canneries diverted much of their fish to reduction plants, because the sardines were claimed to be of inferior quality for canning. The legislature then in session passed a law which prohibited the use of whole fish for reduction without the prior written permission of the Fish and Game Commission. This law also prohibited any cannery from receiving more fish than it could use for canning without spoilage.

The law was tested in two legal cases, one brought against a San Pedro canner who reduced more than the allowable 25 percent overage of whole fish, the other against a Monterey citizen who attempted to operate an independent reduction plant. Both cases were finally tried by the California Supreme Court. The Court's decision upheld the constitutionality of the legislative acts and, further, annunciated the principle that the general right and ownership of the fish are in the people of the state and, consequently, the state has the right to regulate and control the taking and disposition thereof.

Despite these favorable decisions, the control of overage proved difficult until the Fish and Game Commission succeeded in tying overage to case pack by requiring at least 15 cases of 48, 1-pound ovals to be packed per ton of sardines received. The expected case pack from a ton of sardines in good condition is at least 20 cases, hence the ruling allowed 25 percent overage. Later, the allowable overage was increased to 32.5 percent (13.5 cases per ton).

The struggle then entered a new phase. Operators who wished to be straight reductionists put to sea in floating reduction plants, to get beyond the jurisdiction of the State of California. They failed on their first attempt. The *Peralta*, an old concrete vessel, was anchored as a floating reduction plant in Monterey Bay, over 3 miles from shore. The court action taken against the *Peralta* in 1926 resulted in a historic decision concerning territorial jurisdiction over a bay. Monterey Bay, 19 miles between promontories, was found to be completely under the jurisdiction of the State of California. However, a 1927 injunction against the *Lake Miraflores*, a self-propelled vessel equipped as a floating reduction plant and operated 5 miles offshore from San Pedro Bay, resulted in a decision that the vessel, when operated in international waters, was outside the state's jurisdiction. As a result of this decision, *Lake Miraflores* in 1930 began operation as a floating reduction plant outside the continental limits off San Francisco. In 1931, this floating plant processed over 31,000 tons of sardines.

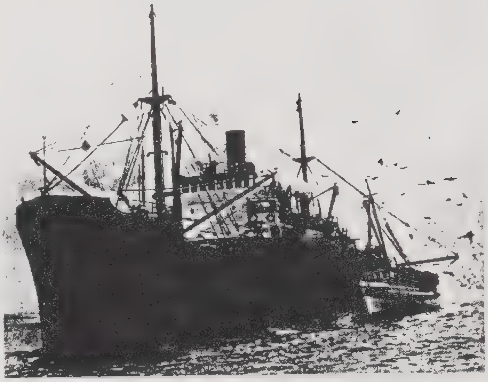
Figure 1. The reduction vessel, *Lake Miraflores*, first to operate outside the continental limit, beyond the jurisdiction of the State of California.

Concurrent with the beginning of the operation of floating reduction plants at sea, the sardine industry ashore was severely affected by the financial depression of the early 1930's. Landings at shore plants had decreased from 325,170 tons in the 1929-1930 season to 133,605 tons in the 1931-1932 season. As canned sardines accumulated in warehouses, canneries had to curtail their operations severely. Sardine fishing boats were put on low catch limits. As noted by Schaefer et al. (1951), it became common practice for the fishermen to bring in more fish than had been ordered, on the off chance that the excess fish could be sold. The immediate reaction of the Fish and Game Commission was an order to fishermen requiring them to avoid taking more fish than they could sell. This action merely intensified pressures to alleviate the economic plight of fishermen and plant operators by relaxing the restrictions on reduction of whole fish. The Fish and Game Commission then, as an emergency measure, decided to grant to each plant making application a permit to reduce up to 7,500 tons of sardines for the manufacture of edible oil and meal during the 1932-1933 sardine season. Soon after the close of the 1932-1933 sardine season, the California Legislature amended the law relative to use made of reduction products, permitting their sale for any purpose. This change permitted the operation of straight reduction plants.

The granting of reduction permits to shore plants did not immediately curb the activity of the reduction vessels. A second vessel, *Lansing*, joined *Lake Miraflores* in 1932. The peak of the offshore operation was reached in the 1936-1937 season when a fleet of nine floating reduction plants processed 235,610 tons of sardines. The competition of the unregulated reduction ships forced liberalization of reduction quotas granted under permit to shore plants. In 1938, the offshore operation was terminated—partly because it had become uneconomical due to increased labor costs, including the requirements of the Seamen's Union for duplicate crews; partly because the supply of fish had fallen off; and partly because of changes in the California law. Several vessels continued to operate, under permit, as dockside reduction plants, however.

The system of reduction under permit meanwhile had become an entrenched part of the California fishery. Reduction was a most profitable operation for more than a decade, including the war years.

Canners had the advantage in tonnage received for reduction. In addition to the tonnage granted under permit, they had the overage of whole fish resulting from the lenient case-pack requirement of 13.5 cases per ton. That this overage was considerable is shown by the canner's performance in later years when reduction was unprofitable. For example, processors obtained 22.2 cases per ton while canning 2.26 million cases during the 1958-1959 sardine season. If this level of performance is a good yard-stick, the overage of whole fish obtained under a case pack requirement of 13.5 cases per ton was over 39 percent. During the height of the reduction period, 1935-1945, sardine case pack averaged about 3 million cases per year, while overage of whole fish from the canning operation averaged approximately 92,000 tons per year (see Table 2).

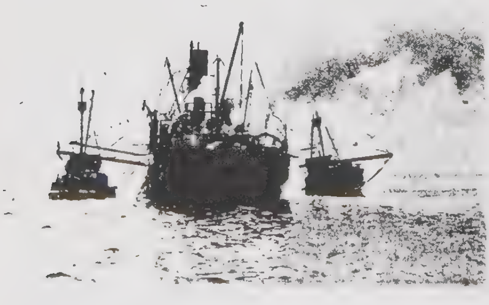

Figure 2. The reduction vessel, *Lansing*, unloading two purse seiners simultaneously.

In the mid-1930's, tonnage allowances under permit for reduction were used only partially. In 1936-1937, the peak season for sardine landings, only 43 percent allowable reduction tonnage was taken; permits were issued to 74 plants, an increase of 54 over the initial 1932-1933 season (Table 3). For several years the number of permits was stabilized at about this level. A small increase in permits took place during World War II, and a marked increase immediately thereafter—to a high of 109 in the 1947-1948 season. In that season the tonnage granted per permit was 2,752 tons, the amount processed was a mere 120 tons. Most of the reduction plants constructed after the war never processed any sardines. A postwar boom in sardine reduction never materialized because the resource had reached too low a level.

Seasonal Limits

Other than control of tonnage of whole fish used for reduction by means of the permit system and case-pack requirements, the principal restriction on sardine fishing in California was its limitation to definite seasons since 1928. The open season differed between the central California and southern California fishing areas:

Open Season: Central California
(Monterey and San Francisco)

1929-30 through 1947-48: Aug. 1—Feb. 15
1948-49 through 1956-57: Aug. 1—Jan. 15
1957-58 through 1960-61: Aug. 1—Dec. 31
1961-62 through 1966-67: Aug. 1—Mar. 1
1967-68 to present: closed

Open Season: Southern California
(San Pedro)

1928-29 through 1942-43: Nov. 1—Mar. 31
1943-44 through 1947-48: Oct. 1—Mar. 1
1948-49 through 1956-57: Oct. 1—Feb. 1
1957-58 through 1960-61: Sep. 1—Dec. 31
1961-62 through 1966-67: Sep. 1—Mar. 1
1967-68 to present: closed

Table 2.—Sardines (tons) processed for canning or for reduction to fish meal and oil by the California sardine industry, 1926-27 through 1965-66 seasons

Season	A Sardines processed[1]	B Reduction under permit	C Taken at floating reduction plant	D Canning tonnage	E Case pack of sardines	F Tonnage required (22.2 cases/ton)	G Whole Fish overage at canneries (D-F)	H Cases per ton (E/D)
1926-27	143,559	0	0	143,559	2,274,310	102,446	41,113	15.8
27-28	181,176	(6,962)[2]	0	174,214	2,623,840	118,191	56,023	15.1
28-29	252,433	(15,728)[2]	0	236,705	2,972,635	133,902	102,803	12.6
29-30	322,600	(24,508)[2]	0	298,092	4,154,640	187,146	110,946	13.9
30-31	182,961	(16,722)[2]	10,960	155,279	2,155,970	97,116	58,163	13.9
1931-32	162,360	(15,979)[2]	31,040	115,341	1,672,160	75,322	40,019	14.5
32-33	248,956	129,473	58,790	60,693	823,980	37,116	23,577	13.6
33-34	381,662	170,155	67,820	143,687	1,957,760	88,187	55,500	13.6
34-35	592,786	342,637	112,040	138,109	1,876,620	84,532	53,577	13.6
35-36	557,996	169,629	150,830	237,537	3,216,915	144,906	92,631	13.5
1936-37	723,751	274,258	235,610	213,883	2,989,045	134,642	79,241	14.0
37-38	413,414	183,858	67,580	161,976	2,300,430	103,623	58,353	14.2
38-39	572,466	337,849	43,890	190,727	2,573,775	115,936	74,791	13.5
39-40	531,878	303,426	0	228,452	3,134,970	141,215	87,237	13.7
40-41	454,709	223,587	0	231,122	3,116,465	140,381	90,741	13.5
41-42	583,463	211,625	0	371,838	5,155,115	232,212	139,626	13.9
42-43	501,341	229,334	0	272,007	3,704,890	166,887	105,120	13.6
43-44	473,522	241,733	0	231,789	3,150,275	141,904	89,885	13.6
44-45	548,415	277,098	0	271,317	3,656,455	164,705	106,612	13.5
45-46	396,090	137,867	0	258,223	3,750,545	168,943	89,280	14.5
46-47	227,716	43,367	0	184,349	2,719,275	122,490	61,859	14.8
47-48	110,237	13,126	0	87,111	1,487,320	66,996	20,115	17.1
48-49	159,848	8,157	0	151,691	2,643,585	119,080	32,611	17.4
49-50	335,572	44,216	0	291,356	4,284,740	193,006	98,350	14.7
50-51	355,160	36,487	0	318,673	5,270,990	237,432	81,241	16.5
1951-52	126,541	1,022	0	125,519	2,367,860	106,660	18,859	18.9
52-53	3,615	11	0	3,604	70,560	3,178	426	19.6
53-54	2,620	0	0	2,620	62,955	2,836	0	24.0
54-55	67,142	0	0	67,142	1,391,925	62,699	4,443	20.7
55-56	73,190	0	0	73,190	1,531,545	68,989	4,201	20.9
1956-57	31,737	0	0	31,737	732,680	33,004	0	23.1
57-58	20,490	0	0	20,490	479,285	21,589	0	23.4
58-59	101,567	0	0	101,567	2,256,600	101,649	0	22.2
59-60	35,364	0	0	35,364	777,500	35,022	342	22.0
60-61	27,078	0	0	27,078	635,695	28,635	0	23.5
1961-62	22,332	0	0	22,332	504,380	22,720	0	22.6
62-63	1,607	0	0	1,607	48,250	2,173	0	30.0
63-64	1,350	0	0	1,350	36,225	1,632	0	26.8
64-65	4,359	0	0	4,359	111,035	5,002	0	25.5
65-66	–[3]	0	0	–[3]	4,320	195	–	–

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[1] Excludes sardines used for purposes other than canning or reduction.

[2] Before the 1932-33 season reduction of sardines permitted only for manufacture of products for human consumption under Fish and Game permit.

[3] Exact tonnage not available, most sardines obtained in loads of mixed fish.

Table 3.—Tonnage granted under permit for sardine reduction in California and tonnage processed by unregulated reduction vessels

Season	Number of permits issued	Total tonnage granted	Tonnage granted per permit	Total tonnage used	Tonnage processed by offshore reduction vessels	Number of reduction vessels	Average tonnage per floating plant
1930-31	0	–	0	0	10,960	1	10,960
1931-32	0	–	0	0	31,040	1	31,040
32-33	20	150,000	7,500	129,473	58,790	2	29,395
33-34	–[1]	–[1]	6,000	170,155	67,820	4	16,955
34-35	–[1]	–[1]	12,000	342,637	112,040	3	37,347
35-36	–[1]	–[1]	4,320	169,629	150,830	4	37,708
1936-37	60	637,500	11,500	274,258	235,610	9	26,179
37-38	74	765,500	var[2]	183,858	67,580	6	11,263
38-39	70	485,764	var[3]	337,849	43,890	6	7,315
39-40	69	402,375	var[4]	303,426	0	0	0
40-41	70	350,000	5,000	223,587	–	–	–
1941-42	74	343,684	4,750	211,625	–	–	–
42-43	76	378,634	4,750	229,334	–	–	–
43-44	75	370,272	4,750	241,733	–	–	–
44-45	78	390,000	5,000	277,098	–	–	–
45-46	85	394,995	4,647	137,867	–	–	–
1946-47	101	394,910	3,910	43,367	–	–	–
47-48	109	299,968	2,752	13,126	–	–	–
48-49	74	99,958	1,350	8,157	–	–	–
49-50	101	75,040	743	44,216	–	–	–
50-51	102	149,997	1,470	36,487	–	–	–
1951-52	84	149,994	1,786	1,022	–	–	–
52-53	60	99,990	1,666	11	–	–	–
53-54	0[5]	0	0	0	–	–	–
				3,378,915	778,560		

[1] Information not available on number of permits issued or on total tonnage granted under permit for the 1933-34 through 1935-36 season. Minutes of meetings of California Fish and Game Commission were checked for these years, but only partial information on the number of permits granted was contained in the minutes.

[2] Permit tonnage based on plant capacity—12,500 or 16,500 tons.

[3] Permit tonnage based on plant capacity—7,000, 9,500, or 13,000 tons.

[4] Permit tonnage based on plant capacity—5,000, 7,500, or 10,000 tons.

[5] No permits issued subsequent to the 1952-53 season.

This legislation on seasons initially was requested by the sardine industry to restrict operations to the portion of the year when fish were most available and in prime condition for canning or reduction.

Scientific Investigations

Up to this point we have dealt mostly with regulations applied to the sardine fishery in California but not with the scientific basis for these regulations. A number of research agencies have contributed to the scientific investigation of the Pacific sardine resource.

The California Department of Fish and Game began research on the sardine fishery over 50 years ago (1918), the Fishery Research Board of Canada in the late 1920's, the Bureau of Commercial Fisheries in 1937, and Oregon and Washington at about the same time. In 1949, a greatly expanded research program, known as the California Cooperative Oceanic Fisheries Investigations (CalCOFI), was undertaken under the sponsorship of the California

Marine Research Committee. Participating scientific groups included the California Department of Fish and Game, the Bureau of Commercial Fisheries, Scripps Institution of Oceanography, California Academy of Science, and later the Hopkins Marine Station of Stanford University.

Hundreds of research papers have been published about the sardine. Perhaps as much is known about the population structure, distribution, recruitment, and ecology of this fish as of any pelagic marine resource. Little of this information has been used in the management of the fishery. In fairness to management, let it be pointed out that much of the information was available only after the abundance of the resource had decreased markedly.

Scientists working on sardine research problems realized the need for communication and cooperation. From the early days of the fishery, scientists from British Columbia and California exchanged information. In 1938, scientists from the states of California, Oregon, and Washington, the province of British Columbia, and the Bureau of Commercial Fisheries met in the first of a continuing series of annual sardine conferences to discuss research results and plan for future research, often cooperatively. After the initiation of the CalCOFI in 1949, the annual sardine conference was merged with the annual CalCOFI Conference.

Scientists of the California Department of Fish and Game warned about the overutilization of this resource and sought to impose a limit of 200,000 to 300,000 tons on the catch. For a time their warnings were heeded; according to Scofield (1934, p. 50) the Fish and Game Commission in 1929 made a policy decision to limit the total catch of sardines to 200,000 tons. Unfortunately, the Commission never really implemented this decision due to a series of emergency actions resulting from the success of the offshore floating reduction plants and the desperate plight of the sardine industry during the early depression years. Emergencies never really ended; no sooner had the offshore reduction vessels been brought under control than World War II began and the United States became involved in 1941. By the time the war ended, the resource already had begun its decline.

It should be pointed out that, when the California Fish and Game Commission made its policy decision in 1929 to limit landings of sardines to 200,000 tons, it had no legal basis for enforcing such a limit. The Fish and Game Commission could then control only tonnage used for reduction (including overage from canning). At no time did it have control over tonnage actually put into cans. Van Cleve (1944, p. 49) pointed up this lack in the biennial report of the California Bureau of Marine Fisheries covering the 1940-1941 and 1941-1942 seasons: "When regulation is finally undertaken, it must be in the form of control of the total catch. The total catch is not controlled by present restrictions, which curtail only the number of tons of sardines taken for straight reduction and are insufficient for proper management."

Several times over the period of the sardine fishery, the California Fish and Game Commission sought a delegation of authority from the legislature to regulate all phases of the fishery. An urgent request was made for such authority in November 1953, for example, after the second dramatic collapse of the sardine fishery in 1952-1953. Such authority still has not been delegated to the Commission.

Population Dynamics

Excellent contributions have been published on the population dynamics of the sardine, including Clark (1939), Widrig (1954), Schaefer (1954), Clark and Marr (1955), Marr (1960), Radovich (1966), Murphy (1966), and Hayasi (1968). We single out Murphy (1966) for comment, as his paper is a synthesis of much of the information learned about the sardine over the years. Observations made by Murphy point up the causes of the decline of the sardine population. Baldly stated, they were overfishing in conjunction with poor survival of some year classes and competition from a flourishing population of northern anchovies, *Engraulis mordax*.

Age composition data of commercial sardine landings had been taken routinely at all ports since 1941, and were available in a less complete form for seasons back to 1932-1933 (Walford and Mosher, 1943; Felin and Philipps, 1948; Mosher and Eckles, 1955; Wolf, 1961. . . .). Using these data, Murphy estimated the maximum sustainable yield of the pre-1949 population (especially between 1937 and 1945) as 471,000 tons at a spawning population size of about 1 million tons. During this period the catch averaged 570,000 tons. Murphy's work indicated that the spawning stock varied considerably above and below the optimum level during these years. The biologically optimal yield (yield so controlled as to restore and keep the population at its optimum level) also would vary considerably.

A highly significant contribution to our understanding of the population structure of the sardine resource was made by Sprague and Vrooman (1962). Using serological techniques, they demonstrated that the frequency of a blood group system, called by them the "C" system, could be used to distinguish between a northern and southern subpopulation of sardines off the coast of California and Baja California. Vrooman (1964) showed that sardines in the Gulf of California made up a third, genetically distinct subpopulation. Murphy made use of information on subpopulations in explaining the rapid decline of the post-1949 sardine population. The northern race appears to have been much larger than the southern, but also more heavily fished. One consequence of heavy fishing was the reduction in numbers of older individuals in the population to a level where they no longer provided an effective cushion against "reproductive failures." Such a reproductive failure of the northern stock occurred in 1949 and possibly 1950. This stock, lacking the resilience supplied by older fish, collapsed, thus accelerating the decline of the sardine resource. Population parameters changed appreciably with the reversed dominance of the two races. For example, the instantaneous rate of natural mortality rose from approximately 0.40 to about 0.80.

At about the same time that the northern race began its catastrophic decline, the anchovy population began to increase spectacularly, moving into the environmental void created by the decline of the sardine. The documentation of the marked increase in abundance of the anchovy population as the sardine population decreased was one of the highly significant accomplishments of the CalCOFI Program (Ahlstrom, 1966, 1967).

The evidence grows stronger that the Pacific sardine was a rather recent acquisition to the pelagic fish fauna of southern California and that it has been subject to marked fluctuations in abundance. Fitch (1969) failed to find any trace of sardine remains in Pliocene and Pleistocene deposits of marine origin in southern California, whereas otoliths of northern anchovy were in every sample examined (three Pliocene, seven Pleistocene), sometimes in considerable numbers. A few fragments of otoliths of young sardines were obtained from Indian middens, but, even there, otoliths of northern anchovy were much more abundant. Soutar (1967) and Soutar and Isaacs (1969) who investigated fish remains, particularly scales, in sediment cores from anoxic basins, gave particular attention to the Santa Barbara Basin off southern California. Sardine scales were much less abundant in the anaerobic sediment cores than those of northern anchovy or Pacific hake and much more variable in abundance during a sedimentation period estimated to cover the past 1850 years.

Murphy's estimate of the parameters of the sardine population, during the period 1952-1960, gave a maximum yield of 57,000 tons at a population of 178,000 tons. He warned, however, that the increase in the anchovy population would surely alter the parameters of the sardine in such a way as to reduce the maximum sustainable yield: "As a converse, the present situation is not likely to alter rapidly, even if sardine fishing is stopped, unless man or nature acts to reduce the anchovy population somewhat. It appears that judicious utilization of all ecologically similar species within a trophic level offers the only hope for sustained yields."

We concur in this appraisal. If the objective is to maximize the catch or the economic value of the catch of abundant fishery resources and minimize the adverse effects of selective fishing (of which the sardine is a nearly perfect example), it will be imperative to encourage "the judicious utilization of all ecologically similar species within a trophic level."

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7103

Fish Fauna of the Western Caribbean Upper Slope

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The importance of studies concerning offshore benthic marine habitats and associations of animals is gradually being realized. The concept of the marine environment is changing from one of extensive, homogeneous habitats with vague boundaries and randomly dispersed individuals, to one of diverse and well-defined habitats which closely control the composition and distribution of associated faunas. Basic descriptions of these distributions are required as bases for more advanced ecological investigations.

Previously a qualitative and quantitative description of the total upper Continental Slope fish fauna in a tropical region has not been available. It is the purpose of this paper to provide such a description for the western Caribbean Sea.

Although the general nature of the Continental Slope fauna has been known since the early days of modern deep-sea exploration (e.g., Agassiz, 1888), little new knowledge concerning the biology of this major environment has been contributed since the turn of the century. As part of a program to expand the commercial fisheries of the United States, the U. S. Bureau of Commercial Fisheries has conducted exploratory trawling surveys of the upper-slope environment in the Gulf of Mexico and off southeastern United States since 1950. Early findings were encouraging and additional work showed that commercial concentrations of the red shrimp, *Hymenopenaeus robustus*, occurred in the northern Gulf and off southwestern and eastern Florida (Springer and Bullis, 1954; Bullis, 1956; Bullis and Rathjen, 1959; Bullis and Cummins, 1963; Thompson, 1967; and Roe, 1969).

Subsequently, explorations were extended to the Caribbean and Cayman Seas, Bahamas, Greater and Lesser Antilles, and off northeastern South America. These continuing surveys have furnished data for an initial assessment of the upper-slope fauna for most of the tropical western Atlantic between Cape Hatteras, North Carolina and the easternmost tip of Brazil. Some areas of high productivity have been effected off the east coast of Florida in an area 1.6 to 3.2 km wide between 29° and 30° north latitude. In addition to the field records, representative samples of the fauna have been, and are presently, routinely collected and distributed to cooperating systematists. Results of these surveys and laboratory identifications are incorporated into the automatic data retrieval system of the Bureau's Pascagoula, Mississippi Exploratory Fishing and Gear Research Base. Faunal lists and capture records from all phases of the exploratory fishing program are periodically published (Springer and Bullis, 1956; Bullis and Thompson, 1965). The history and activities of the program have been recently summarized by Bullis (1964).

Two exploratory fishing surveys of the upper slope in the western Caribbean were made by the R/V *Oregon* Cruise 46 in late summer of 1957 and Cruise 78 in late spring of 1962. On the first cruise, field data were incomplete and emphasis was on obtaining extensive qualitative collections of fishes and invertebrates. The identified collections from the first cruise enabled detailed records of species occurrence and abundance to be maintained during the second cruise. These are reported and discussed here.

STUDY AREA

The study area is shown in Fig. 1 along with the locations of the 44 stations evaluated in this report. Observations were made in the 75- to 500-fathom depth range in four general areas; off Rosalind Bank, northern and southern Nicaragua, and western Panama. This is a north-south distance of about 800 km and encompasses most of the western Caribbean.

The Continental Shelf within the northern portion of the area is roughly triangular, narrowing to less than 32 km at the western and southern extremities and broadening to some 200 km between Cabo Gracias a Dios and the northeastern corner.

The shelf proper is a limestone bank, for the most part, with depths from 10-30 fathoms. It is heavily covered with surface or near-surface reefs and many cays (keys) within the 20-fathom isobath. The bottom is irregular and covered with sponge and corals beyond the 20-fathom isobath, making sampling with a trawl, or even a dredge, difficult. Within the 10-fathom isobath are extensive stretches of smooth bottom, consisting mostly of sand and calcareous mud, and here considerable commercial shrimp trawling is conducted periodically.

The shelf edge, or break, varies from 30-40 fathoms below the surface. The bottom to depths of 75-100 fathoms is very rough and

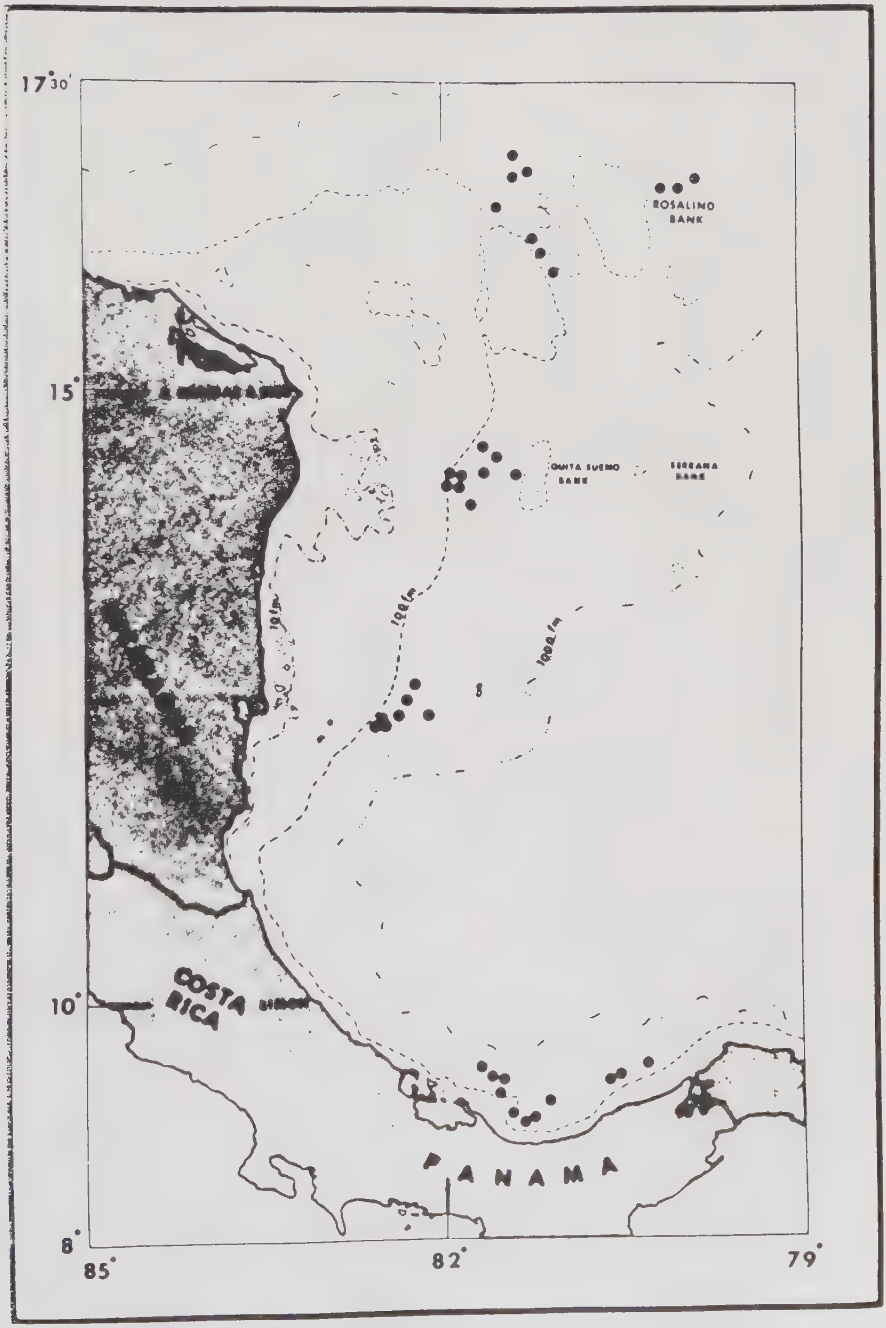
17°30'
ROSALINO BANK
15°
QUITA SUENO BANK
SERRANA BANK
100fm
1000fm
1000fm
100fm
COSTA RICA
10°
PANAMA
8°
85°
82°
79°

Fig. 1. Study area in the southwestern Caribbean Sea showing positions of trawl stations during R/V *Oregon* Cruise 78. Each dot represents one or more stations.

also generally untrawlable. Along the northern edge of the shelf, the upper Continental Slope has temperature gradients of 3-18C; the distance between the 75- and 500-fathom isobaths ranges from 3.2-2.2 km. A large bank about 56 km long and several small banks, all less than 20 fathoms deep, are connected to the northeastern corner of the shelf by depths of 100-150 fathoms. A 16- to 24-km wide channel with depths of 250 to 400 fathoms separates the large bank from Rosalind Bank to the northeast. Northwest of the channel between the Continental Shelf and Rosalind Bank there is a broad, flat area, seemingly a submarine alluvial fan, of about 100 square km at a fairly consistent depth of 150 fathoms.

South of Rosalind Bank the Continental Slope is broad all the way to about 12° north latitude. The horizontal distances between the 100- and 1,000-fathom isobaths range from 105-39 km, with an average of about 76 km. Within these limits are several large banks and small islands. Serranilla Bank (16°N, 80°W) and Quita Sueno Bank (14°30′N, 81°W) are separated from the shelf by depths less than 500 fathoms. The other major structures, Serrana and Roncador Banks and Old Providence and St. Andrews Islands, are separated from the shelf by depths of 800 fathoms or more. The distance of the 500-fathom isobath from the shelf edge is 63 km at the northern end (15°N), 21 km at 13°30′ north latitude, 51 km at 13° north latitude, and about 13 km off Bluefields, Nicaragua at 12° north latitude. Between 15°N and 12°30′ north latitude the slope gradient is very gentle, ranging from less than 1° to about 4°. The bottom there consists of gray and white mud. The sampling and sounding transects run by the R/V *Oregon* indicate that this area offers several thousand square km of good trawling bottom. South of 12°30′ north latitude the slope is steep and rough, with numerous precipitous faces and gullies to depths of at least 500 fathoms. The bottom is calcareous.

The Continental Shelf in the Golfo de los Mosquitos is narrow, averaging 8-16 km wide, and has a topography and bottom invertebrate fauna similar to the shelf off eastern Nicaragua. The upper slope has a moderate smooth gradient, as off most of Nicaragua, and, in general, no trawling difficulties were encountered.

Temperatures

The western boundary current is the dominant hydrographic feature in the West Indian region. This system is composed of extensions of the equatorial currents that enter the eastern Caribbean Sea over the Antilles Ridge. The strong, mixed Caribbean current passes through Cayman Sea and the Yucatan Channel, turns easterly and then flows through the Straits of Florida with increased velocity, emerging as the Florida Current. This current follows the southeastern coast of the United States to Cape Hatteras where it leaves the coast, and, with the union of the Antilles Current, it becomes the Gulf Stream. Along the edges of this system numerous eddies develop, especially in the southwestern Caribbean and Cayman Seas and between Jamaica and Cuba. There are also several large, apparently semi-permanent, eddies in the Gulf of Mexico (Sverdrup, Johnson, and Fleming, 1942).

This warm, northerly flowing current has a profound influence on the Continental Shelf fauna of the region and accounts for the northerly extension of established populations of tropical animals into the Gulf of Mexico and to Cape Hatteras at 35°20′ north latitude (Ekman, 1953, p. 46; Cerame-Vivas and Gray, 1966; Struhsaker, In Press). As Cerame-Vivas and Gray point out, these warm, western boundary currents result in the characteristic "trumpet shape" faunal distributions of the tropical regions of the world ocean.

In a different manner, the western boundary current greatly influences the West Indian upper-slope fauna. Because of the density relations within a stratified fluid in motion in the Northern Hemisphere (when looking at a cross-section of the current in the direction it is flowing) the lighter (warmer) water lies to the right of the current and the denser (colder) water lies to the left. This results in a strong horizontal temperature gradient maintained by a cross circulation that advects warm water on the right side of the current, while cold, deep water is brought near the surface on the left side of the current (Dietrich, 1963, p. 535). Thus, the upper slopes of the continental Western Hemisphere have temperatures of 8-12 C at depths of 220 fathoms, whereas temperatures of 14-17C are found at the same depth over the upper slopes of the Bahamas, Greater Antilles, and much of the Lesser Antilles (see Chart V of Sverdrup, Johnson, and Fleming, 1942). Struhsaker (In Press) has pointed out that this results in two natural divisions of the upper-slope environment in the tropical western North Atlantic, which may be termed the Continental Slopes and the Insular Slopes. Exploratory trawling surveys have shown striking differences between the faunal composition of the two divisions at similar depths. That species common to both divisions occur much deeper over the Insular Slopes is also readily apparent. This effect seems to be exceptionally well demonstrated in the Straits of Florida where the two major divisions of slope faunas of the region occur on opposite sides of the Straits, only about 65 km apart. We hope this paper will provide some basis for the eventual detailed analyses and comparisons of the two faunal divisions.

Normally, bottom temperatures at the 100-fathom isobath of the Continental slopes (hereafter distinguished from the Insular slopes) range between 15-21 C, whereas at 200 fathoms temperatures are from 8-12 C. Eighteen bottom temperatures were obtained during the survey with an experimental minimum temperature recording device that was previously calibrated with a protected thermometer. The results are shown in Fig. 2 along with data on indicated bottom temperatures in the study area from Parr (1937). The resulting bottom temperature profile for the study area agrees well with the temperatures presented by Fuglister (1960) and Stewart (1962) for this region.

Because of the temperature gradients in the western boundary current as mentioned above, the deep permanent thermocline layer (PTL) of the western North Atlantic, is centered at about 200 fathoms here (Struhsaker, In Press). As Fig. 2 shows, the PTL (between about 19-7C) encompasses most of the upper Continental Slope zone in the study area. Although the upper-slope bottom temperatures are below the depth of seasonal influences, Struhsaker (In Press) presented evidence that internal waves in the PTL could effect short-period temperature changes of at least 3 C. He also hypothesized that these temperature changes might effect local changes in the depth distribution of some of the more mobile inhabitants of the upper slopes.

METHODS

The sampling gears used in this study were 12.2 m flat and semiballoon shrimp trawls (Bullis, 1951). The netting was 5 cm stretched mesh (#18 thread cotton) in the trawl bodies and 4 cm stretched mesh (#42 thread cotton) in the codends. These trawls cover a path 6.7-7.3m wide under usual conditions when spread with 1.8 m trawl doors. Using a single float, the trawl has a vertical opening of about 1.5 m. The footrope rides very lightly on the

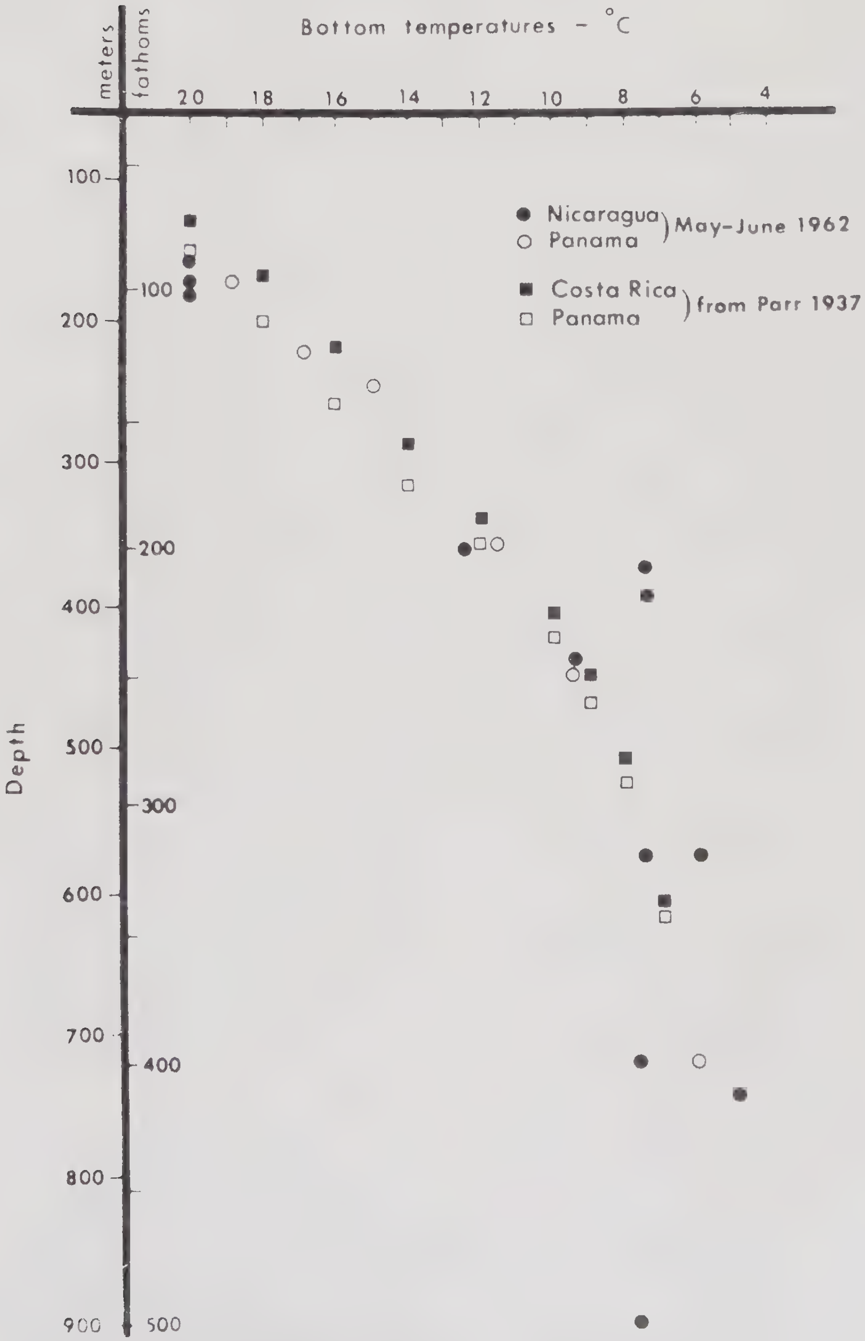

Fig. 2. Bottom temperature profile for Continental Slope depths in the southwestern Caribbean Sea.

bottom and a "tickler chain" attached to the bottom rear corner of each door rides about .6-.9 m in front of the footrope and incites the more active benthos to swim or jump off the bottom into the path of the trawl.

Because of the number of variables involved, quantitative data on animal populations sampled with shrimp trawls can be developed only in very general terms. Sampling periods of 1, 2, 3, and 4 hours were attempted, but frequently they were interrupted because trawling hazards appeared on the depth sounder-recorders. Navigation was by celestial means and loran fixes except in a few cases of radar positioning. We attempted to maintain a constant speed of 2 to 3 knots (1.0-1.4 m/second) but current conditions may have varied the range of speeds as much as ±2 knots (1 m/second) in some areas. Quantifying these data is further complicated because shrimp trawls capture only a portion of the animals in their paths. For example, recent motion picture analyses (unpublished) of shrimp trawl performance by the Bureau of Commercial Fisheries Gear Research Unit, Pascagoula, Mississippi, show that escapement of royal-red shrimp (*Hymenopenaeus robustus*) might be as high as 90 per cent of all shrimp encountered by the trawl.

Despite these difficulties, some attempt must be made to quantify and interpret these observations on the upper-slope fauna to provide bases for more detailed and sophisticated investigations. Until more efficient sampling gears are devised, we feel that analysis of a large number of shrimp trawl samples will provide some of these bases. Because of the known inefficiency of the trawls, all biomass and numerical density figures given in this paper should be considered minimal. To determine the area sampled in each depth range, we assumed an average on-bottom trawl speed of 2.5 knots (1.2 m/second) and average net opening of 7 m, which resulted in a sampling rate of 3.2 hectares per hour.

The amount and distribution of sampling effort and the numbers and weights of fishes taken are shown in Table 1. Fifty-fathom depth intervals were selected as the most practical because of sampling distribution. The number of stations in each 50-fathom depth range varied from 1-9, whereas the number of hectares sampled varied from 9.6-60.8. The 44 trawling stations represent a total of 79.6 hours of on-bottom sampling time during which about 29,700 fishes were captured. At each station the fishes and the crustaceans were sorted from the catch and counted. Lengths and

TABLE 1

Distribution of Sampling Effort, Number of Families, Number of Fish taken, Pounds of Fish taken, Density and Biomass by Depth in the Study Area

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Total no. stations	6	9	8	9	3	4	2	1	2
Total no. hectares sampled	19.2	34.9	60.8	49.6	20.8	30.7	13.1	9.6	16.0
Total no. of families taken	31	36	37	41	33	34	18	8	8
Total no. of fish taken	1827	3967	9796	9451	1838	2176	422	25	174
Average no. of fish/ hectare sampled	95.2	113.7	161.1	190.5	88.4	70.9	32.2	2.6	10.9
Total no. of kgs. of fish taken	150	218	350	418	104	150	45	9	27
Average no. of kgs./hectare	7.8	6.2	5.8	8.4	5.0	4.8	3.4	1.0	1.7

weights were recorded for most species of the readily identifiable fishes. Measurements were made using measuring boards with 0.5 cm units. Extensive zoological collections were made during the survey, most of which are in the collections of the U. S. National Museum and the Bureau's Tropical Atlantic Biological Laboratory, Miami, Florida.

RESULTS AND DISCUSSION

Composition, Abundance, and Distribution. Any attempt to report on a large portion of the slope fauna of the western Atlantic south of 35° north latitude is complicated by the limited taxonomic knowledge of many important groups of animals and lack of identification keys suitable for field use. An extreme example of the unknown nature of the fish fauna in the study area is represented by the Scyliorhinidae (See Appendix I). This family was represented by four forms; *Galeus arae*, a new species of *Galeus*, a new species of *Scyliorhinus*, and an undescribed genus and species. Springer (1965) has since described these forms (See Appendix I). Of three species of chimaeras present, only one, *Hydrolagus alberti*, has been recorded as a member of the western Atlantic fauna. A second species of *Hydrolagus* probably represents what has been considered an endemic of the northwestern Atlantic, and the third an undescribed species of *Neoharriotta* (Bullis and Carpenter, 1966), previously considered a monotypic genus in the eastern Atlantic. Other groups that presented identification problems were the families Congridae, Brotulidae, Gadidae, and Ophidiidae, and the peristediid genus *Peristedion*.

The benthic fishes taken during the survey represent 60 families and an estimated 140 species; however, in the field only about 73 were identified to species, 21 to genera and the remainder to family. All of the batoid fishes were preserved and later identified by William C. Schroeder, Woods Hole Oceanographic Institute. These field and laboratory identifications resulted in a total of 127 species and species groups of demersal fishes, which are listed in Appendix I.

We should state here that we consider all fishes listed to primarily occupy the demersal habitat as adults. Thompson (1963) considers the bathyalbenthic bottom community to be a richly populated ecotonal belt, which grades into the pelagic layers above and the benthic layers below. The belt is inhabited not only by endemic species, but also occasionally by truly benthic or pelagic animals. Fish inhabitants of this belt are easy to capture in our bottom trawls; therefore, we consider demersal fish species to be not only those that rest upon or burrow in the bottom but also those that are free-swimming but still closely associated with the bottom.

In general composition, some 75 per cent of the identifiable species taken in the study area are widely distributed at similar depths along the Continental Slopes of the tropical western Atlantic region. About 18 per cent of the species appear to be approaching the southern limit of their geographic range; 3 per cent are nearing the northward limit; and the remaining 4 per cent are known only from the southwestern Caribbean. Therefore, 93 per cent of the western Caribbean species are found in the Gulf of Mexico and along the southeastern coast of the United States, whereas only 78 per cent are known from the southeastern Caribbean and off northeastern South America (as derived from available literature sources and extensive unpublished distribution data at the Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi).

The depth distribution and numerical abundance of each family and species group is given in Appendix I. The relative abundance of each family and the bottom temperatures in each 50-fathom depth zone are shown in Figs. 3a and 3b. Families that were present, but comprised less than 1 per cent of all the fishes taken, are shown as a straight line, whereas the dashed line indicates that the family was not represented in that depth range.

Fifteen families were numerically dominant in the study area. Seven of these achieved dominance by the abundance of single species: Caproidae—*Antigonia combatia*; Polymixiidae—*Polymixia lowei*; Triglidae—*Bellator egretta*; Zeidae—*Zenion hololepis*; Grammicolepidae—*Xenolepidichthys dahlgleshi;* Neoscopelidae-*Neoscopelus macrolepidotus*; and Chaunacidae—*Chaunax pictus*. The remaining eight families achieved their dominant status by the occurrence of from 2-14 species.

Upon leaving the shelf, 26 per cent of the families represented in 75-100 fathoms are lost. At 150 fathoms 39 per cent have been lost; 49 per cent at 200 fathoms; 59 per cent at 250 fathoms; and at 350 fathoms 88 per cent have disappeared. Of the remaining four families, one drops out at 400 fathoms, one at 450, and two persist to the limits of the study depths. However, of 31 families found on the outer shelf (75-100 fathoms), six (Apogonidae, Scorpaenidae, Ogcocephalidae, Brotulidae, Ophidiidae, and Congridae) are composed of diverse species that represent their respective families over a wide bathymetric range, and six additional families (Caproi-

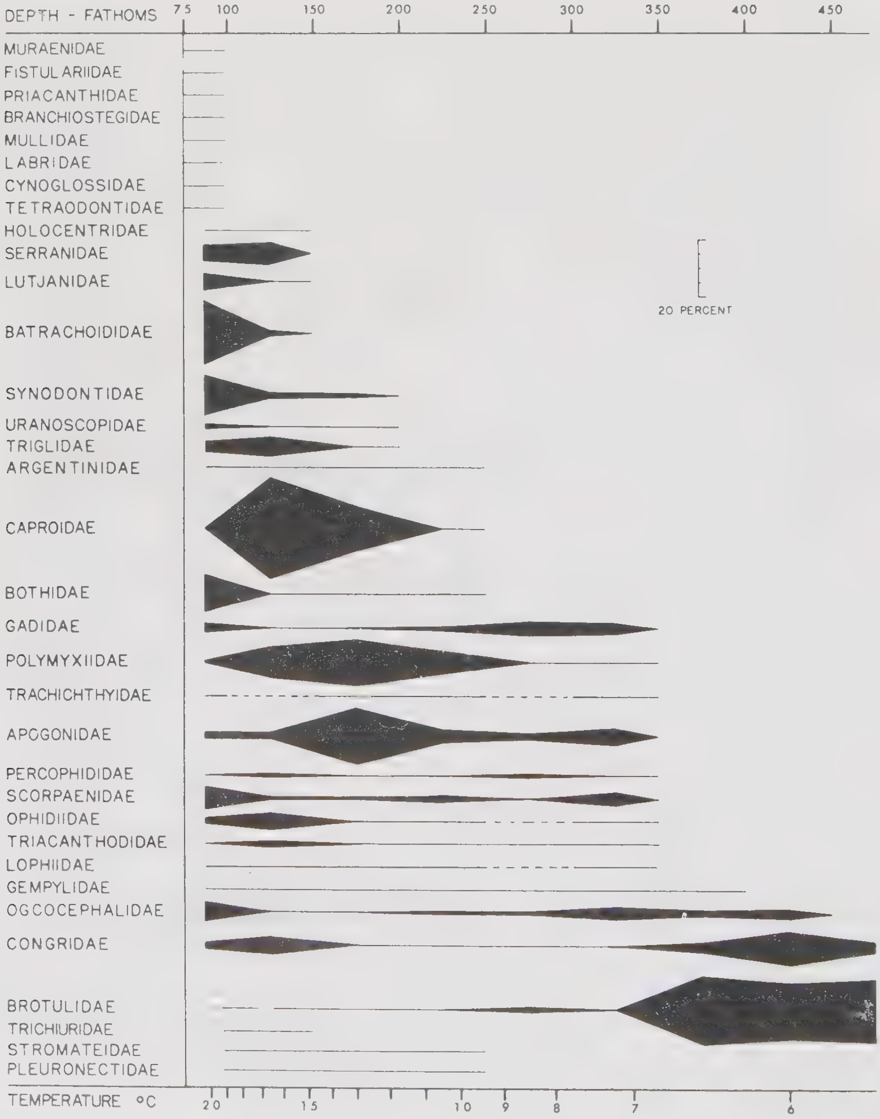

Fig. 3a. Relative abundance of families on the Upper Continental Slope of the southwestern Caribbean Sea as percentage of total fishes sampled from each depth range.

dae, Triacanthodidae, Percophididae, Polymixiidae, Trachichthyidae, and Gempylidae) are shallow-water extensions of families that may be considered as typical inhabitants of the upper Continental Slope.

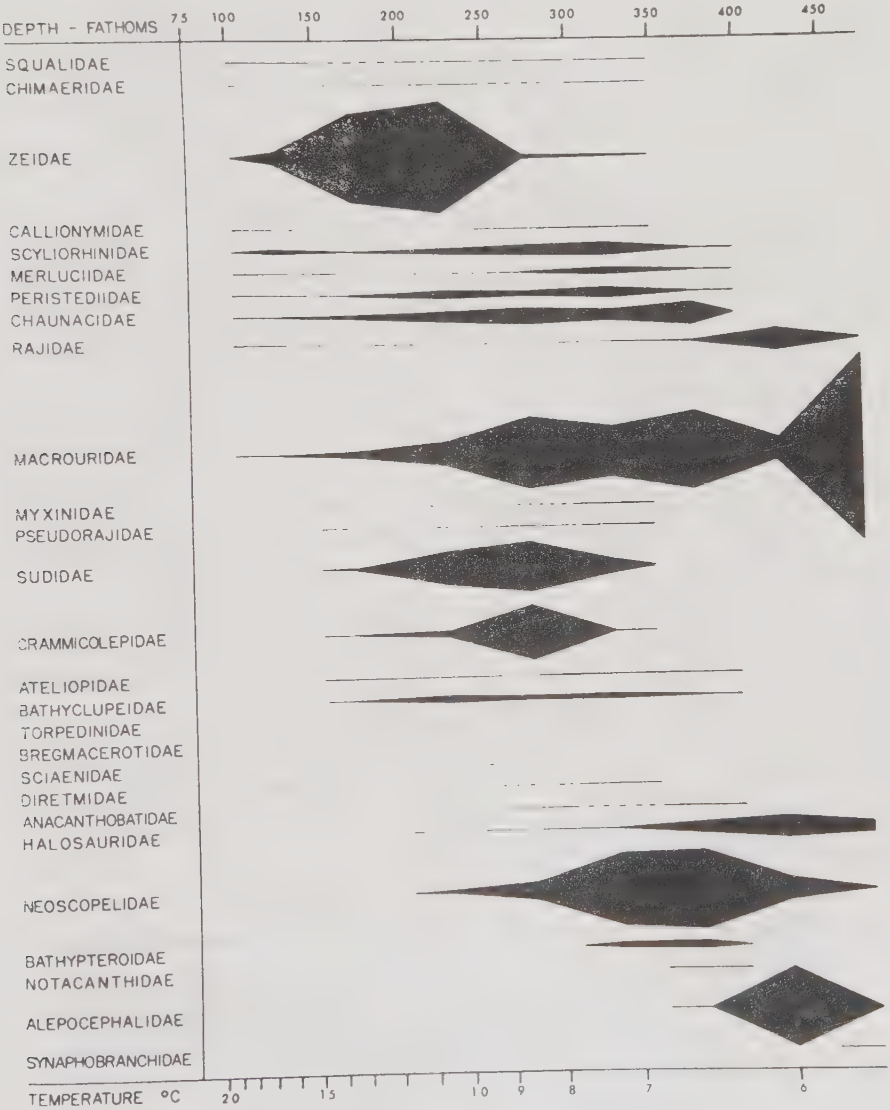

Fig. 3b. Relative abundance of families on the Upper Continental Slope of the southwestern Caribbean Sea as percentage of total fishes sampled from each depth range.

Within the 101- to 150-fathom range, we first find many families that might be considered as typical inhabitants of the upper Continental Slope in the Caribbean region. Nineteen families (Caproidae, Triacanthodidae, Percophididae, Polymixiidae, Anacanthobatidae, Pseudorajidae, Merluciidae, Callionymidae, Scyliorhinidae, Peristediidae, Zeidae, Chaunacidae, Sudidae, Chlorophthalmidae, Myxinidae, Bathyclupeidae, Ateleopidae, Chimaeridae, and Neoscopelidae) were taken in the study area. The four numerically dominant families in numbers of individual fish are the Caproidae, Polymixiidae, Serranidae, and Triglidae, respectively. The last two families are typical shelf inhabitants, with some members (i.e., *Serranus phoebe*, *Bellator* sp.) extending slightly beyond the edge of the Continental Shelf.

In the 151- to 200-fathom range the numerically dominant families are all typically upper-slope groups. Four families make up 83 per cent of the total number of fish taken in these depths: Zeidae (32 per cent), Apogonidae (18 per cent), Caproidae (17 per cent), and Polymixiidae (16 per cent). The typical shelf families decrease in number rapidly.

The zeids are still the dominant family in the 201- to 250-fathom range and comprise 39 per cent of the total number of fishes taken in these depths. In abundance, they are followed by the Sudidae, Macrouridae, and Polymixiidae. This marks the first appearance of sudids and macrourids in any numbers. The Caproidae is poorly represented in this depth range, decreasing rapidly in abundance after being the dominant family in 101-150 fathoms.

The Macrouridae comprise 26 per cent of the fish sampled in the 251- to 300-fathom depth range and assume dominance. Large numbers of grammicolepids are present only in this depth range. The Sudidae remain numerically important and are followed by the first appearance of the Neoscopelidae.

The Neoscopelidae assume dominance (27 per cent) in the 301- to 350-fathom depth range and are followed by the macrourids (18 per cent). Most of the remaining fish caught are more or less uniformly distributed among eight families, six of which were typically upper-slope forms. Beyond 300 fathoms the upper-slope families are numerically less important.

The Neoscopelidae and Macrouridae are still the dominant families (28 per cent) each in the 351- to 400-fathom depth range, closely followed by the Brotulidae (24 per cent), which makes its first appearance as a numerically important family. The upper-slope families are virtually unrepresented in this depth range where, along with the brotulids, there is the introduction of the Halosauridae, Congridae, and Bathypteroidae as numerically important groups.

In 401-450 fathoms the alepocephalids and brotulids are dominant and, collectively, account for 48 per cent of the fish taken in this depth. Further net "loss" of families in this depth range reduces the total number of families to eight; however, only one station was occupied in that depth range.

Eight families are present in the 451- to 500-fathom depth range, of which the macrourids are overwhelmingly dominant (68 per cent). The remaining seven families are either typically abyssal or are those with wide bathymetric distributions.

Distribution Pattern. The general pattern that emerges from these abundance and distribution data is typical of most animal aggregations. Although many groups are present in an area, the total faunal composition is dominated by only a few taxa. In passing from one depth zone to another, these dominant taxa arise, gain dominance in a particular zone, and then gradually lose importance and disappear. Although records were not kept on the weights of the species and species groups taken at each station, examination of the numerical density data in conjunction with known weight ranges for each group indicates that when a family is among the numerically dominant in a particular depth range, it is usually one of the dominant groups with regard to biomass.

Although there is, in general, a gradual replacement of one dominant group by another from zone to zone, the data of Fig. 3 seem to show two major trends. The first is the disappearance and appearance of many families between 75 and 100 fathoms. The second is the apparent major loss of families in depths greater than 350 fathoms. This effect is further illustrated in Fig. 4 where the total number of families taken in each depth range is given along with the number of families "gained" and "lost" in each depth range when progressing from lesser to greater depths. The net change for each depth range is shown at the top of its column. The total number of families gradually increases from the shelf edge to a high in the 201- to 250-fathom depth range. The number gradu-

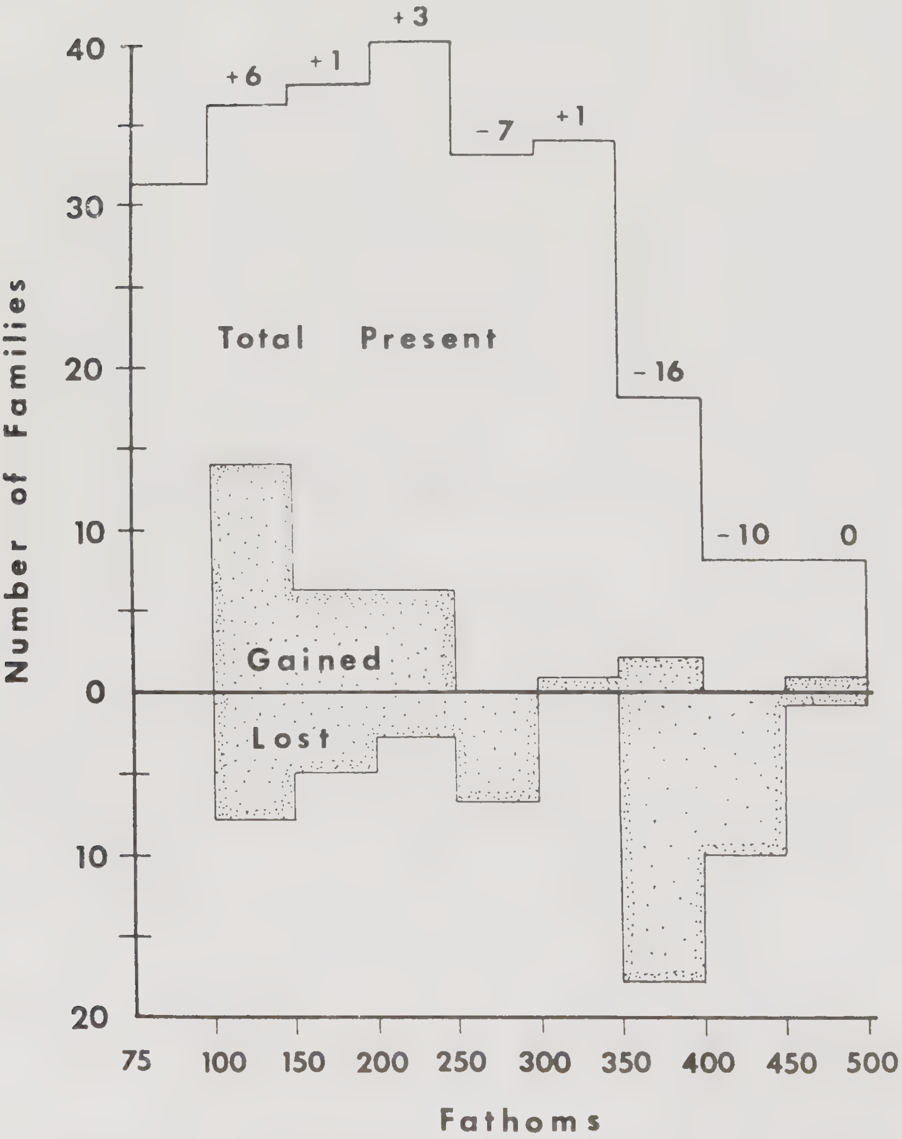

Fig. 4. Total number of families present in each depth range and the number of families "gained" and "lost" in each depth range when progressing from lesser to greater depths. Net change for each 50-fathom interval shown at top of histogram.

ally diminishes in the next two depth ranges, but is suddenly reduced between 351-400 fathoms and 401-450 fathoms.

This pattern is interpreted as follows: upon leaving the shelf, the familial composition of the ichthyofauna undergoes a major

TABLE 2

Estimated Minimum Standing Crop for the Indicated Depth Ranges within the Study Area

Depth range in fathoms	Kilograms/hectare			
	Fish	Crustaceans	Other Invertebrates	Total
75-100	7.8	0.9	3.1	10.9
101-150	6.2	0.3	4.5	11.0
151-200	5.8	1.2	2.0	9.0
201-250	8.4	2.7	1.7	12.8
251-300	5.0	0.9	1.3	7.2
301-350	4.9	1.3	1.5	77.7
351-400	3.5	2.4	0.4	6.3
401-450	1.0	0.0	0.4	1.4
451-500	1.7	0.4	0.7	2.8

change, resulting in an overall gain in families from the outer shelf zone (75 to 100 fathoms). Conditions stabilize in the next few depth ranges: with the small exchange of families that occurs, there is a general increase in the total number of families present to 201-250 fathoms. In the next two depth ranges, however, only one new family is introduced, whereas eight are lost. The great reduction of family numbers between 351 and 450 fathoms is due to the loss of 26 families with only two additions.

The estimated minimal standing crop of fishes within the study area is given in Table 2. The total biomass generally decreases upon leaving the Shelf edge but increases to a peak in the 201- to 250-fathom depth range. Beyond these depths the biomass decreases with depth. Whereas the estimated biomass of fishes follows this pattern, the echinoderms, sponges, and mollusks exhibit a generally decreasing biomass with increased depth. The crustaceans exhibit an increased "standing crop" in the 201- to 250-fathom and 351- to 400-fathom depth ranges. This is probably due partially to quantities of *Hymenopenaeus robustus* and *Nephrops binghami* in the 201- to 250-fathom range and *Plesiopenaeus edwardsianus* in the deeper depth range.

Upper-Slope Association. On the basis of the above data, there appears to be an association of fishes that is characteristic of the upper Continental Slope. The upper limit of this fauna in the 75-

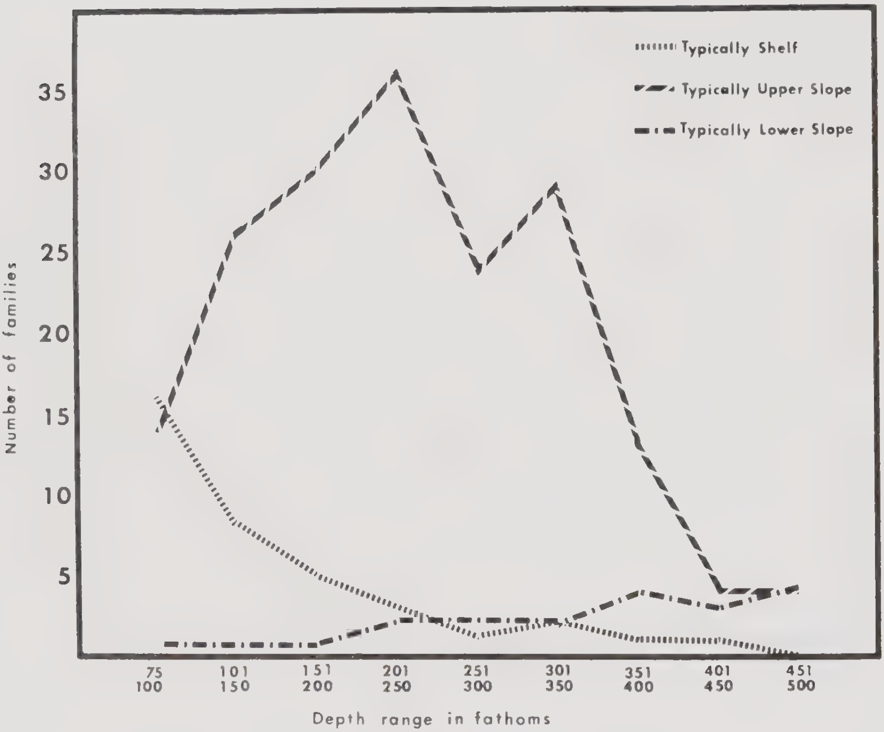

Fig. 5. Numbers of families at descending depth levels considered representative of shelf, upper-slope, and lower-slope ichthyofauna.

to 150-fathom depth range is an exchange area where typically shelf families are replaced by upper-slope families. The lower limit of upper-slope fauna is demarcated by the drastic reduction of total number of families present and replacement of upper-slope families with lower-slope families at depths greater than 350 fathoms. The shelf families are defined here as those that have greatest numerical density in depths between 75-100 fathoms. Upper-slope families are considered to be those that have the greatest density between 101-350 fathoms, and lower-slope families those greatest between 351-500 fathoms. The number of families in each category present in each depth range is shown in Fig. 5. As expected, the number of shelf families greatly diminishes beyond 100 fathoms and none are present in the 451- to 500-fathom depth range. The lower slope families exhibit a similar trend from greater to lesser depths, reaching a peak number between 201-250 fathoms.

Although we have observed this enriched, distinctive upper-slope fauna in other areas of the tropical western North Atlantic, the data presented here represent the first quantitative analysis of this faunal association. In the western Caribbean, this association is distributed roughly between the 19 C isotherm (100 fathoms) and the 7 C isotherm (350 fathoms). These temperatures delimit the deep, permanent thermocline layer of the western North Atlantic region where it contacts the Continental Slope. There the fauna flourishes at depths of the 10 C isotherm (225 fathoms), diminishing quantitatively and qualitatively above and below this depth over the slope.

Schroeder (1955) reported the results of extensive trawling explorations of the Continental Slope in the western North Atlantic between Delaware Bay and Nova Scotia. About 75 species of bottom fishes were taken at 259 trawling stations in depths of about 50-730 fathoms over a two-year period. Of those species listed for the New England slope, the following eight were also taken in the western Caribbean: *Myxine glutinosa, Argentina striata, Parasudis truculentus, Merluccius albidus, Coelorhynchus carminatus, Zenopsis ocellatus,* and *Urophycis regius* (the last species was taken in the western Caribbean, but is not listed in Appendix I because detailed counts were not maintained for it). Schroeder (1955, p. 366) also presented estimates of the standing crop of slope fishes off New England. A comparison of Schroeder's figures (converted to kg/ha) for that region and our values (Table 2) are as follows: 101-200 fathoms, 17.9 vs. 6.0; 201-300 fathoms, 48.1 vs. 6.7; 301-400 fathoms, 50.4 vs. 4.1; 401-500 fathoms, 36.9 vs. 1.3. These data would indicate that the standing crop of fishes on the slope region of the northwestern Atlantic to be about 3, 7, 13, and 28 times as great as in the Caribbean. These data, however, should be compared only in a very general manner because Schroeder's estimates are based on catches of 18.2 m trawls with 7.6 cm mesh webbing, whereas our estimates are based on catches of 12.2 m trawls with 5 cm mesh webbing. As Schroeder (1955, p. 364) points out, bottom trawl catches seem to increase exponentially with increased trawl size. It thus appears that the New England slope ichthyofauna is richer quantitatively, but poorer qualitatively than that of the western Caribbean, as would be expected.

TABLE 3

Mean Lengths (mm) of Fishes Measured by Depth

Depth range (fathoms)	75	101	151	201	251	301	351	
Species	100	150	200	250	300	350	400	(n)
Antigonia combatia (TL)	97	121	—	—	—	—	—	(944)
Bathypterois bigelowi (FL)	—	—	—	—	134	118	123	(58)
Bembrops gobioides (TL)	—	—	195	180	193	—	—	(69)
Chaunax pictus (TL)	—	62	102	118	122	130	190	(1275)
Chlorophthalmus agassizi (TL)	—	—	72	136	148	145	—	(574)
Parasudis truculentus (TL)	—	—	161	205	220	—	—	(104)
Coelorhynchus carminatus (SD)	—	—	54	59	65	59	—	(273)
Cyttopsis roseus (TL)	—	—	—	93	110	—	—	(74)
Galeus arae (TL)	—	—	259	277	251	275	—	(344)
Merluccius albidus (TL)	—	—	275	290	365	415	—	(130)
Neoscopelus macrolepidotus (SL)	—	—	—	—	91	94	126	(762)
Nezumia bairdii (SD)	—	—	48	47	56	52	72	(408)
N. hildebrandi (SD)	—	—	—	32	36	—	44	(253)
Parahollardia schmidti (TL)	—	—	112	138	—	—	—	(90)
Polymixia lowei (TL)	97	129	136	153	127	—	—	(1489)
Setarches parmatus (TL)	—	—	86	103	—	127	—	(368)
Synagrops bella (FL)	—	98	125	158	182	167	—	(717)
Xenolepidichthys dahlgleishi (TL)	—	—	95	102	88	—	—	(324)
Zenion hololepis (TL)	—	59	63	78	71	—	—	(635)

TL, total length; SL, standard length; FL, fork length; SD, tip of snout to origin of first dorsal.

Size and Depth. Extensive size-frequency data were taken for 19 species of fishes. They are summarized in Table 3 as mean sizes for each 50-fathom depth range. Species that were selected are readily identifiable and are a major component of the tropical western Atlantic upper-slope ichthyofauna. With a few notable exceptions, such as the peristidiids, ophidiids, brotulids, gadids, and congrids (most present identification problems now) these species represent a rather typical cross-section of the upper-slope ichthyofauna.

Fifteen species (*Chlorophthalmus agassizi, Parasudis truculentus, Neoscopelus macrolepidotus, Nezumia hildebrandi, N. bairdii, Coelorhynchus carminatus, Merluccius albidus, Cyttopsis roseus, Zenion hololepis, Antigonia combatia, Parahollardia schmidti, Polymixia lowei, Setarches guentheri, Synagrops bella,* and *Chaunax pictus*) demonstrate an increased mean size with increased depth. All but *Chaunax* and *Polymixia* have a significant (at the 1 per cent level) linear correlation. A curvilinear relation for these two species is strongly indicated.

The mean lengths of the four remaining species (*Bathypterois bigelowi, Xenolepidichthys dahlgleishi, Bembrops gobioides,* and *Galeus arae*) are nearly constant at all depths. A positive correlation between size and depth was found in *Galeus arae*. However, a complex distributional pattern in this species related to sexual maturity and depth grouping may bias the data toward this relation (Bullis, 1967).

For the most part, each species reaches its greatest density somewhere toward the center of its depth range. Also, species showing a strong size-depth relationship tend to have greater bathymetric ranges than species that do not demonstrate such a relationship.

The direct relation between size and depth has been discussed in detail for *Pleuronectes* in the North Sea, where such differential distribution also varies inversely between size (age) and density (Graham, 1956). Size increase with depth has been shown for several western Atlantic Shelf species by Caldwell (1955, 1957, 1961).

Explanatory Theories. In seeking an explanation for the above data, the modes of reproduction of the species involved were considered. Teleostean species in which the young develop pelagically characteristically spawn large numbers of eggs, whereas species in which the young develop in demersal habitats produce only moderate to small numbers of eggs (Mead, Bertelsen, and Cohen, 1964). On the basis of these general types of development, the two following hypotheses are given to account for the size-depth relations reported above.

First, species that increase in mean size with increasing depth and decreasing temperatures, and have a broad bathymetric range, produce pelagic eggs and/or larvae. The young of these species are carried various distances along the coasts and may be swept inshore over the Continental Shelves or offshore into oceanic areas. After developing to the pre-juvenile stage, they either descend gradually to some depth or undergo relatively small daily vertical migrations. The depths to which these individuals descend are limited by the temperature tolerances of that species at that particular stage in its life history. Our hypothesis requires that these pelagic young do not descend deeper than the Continental Shelves or the upper end of the species' demersal depth range on the upper slope. Individual pre-juveniles undergoing vertical movements over the shelf and upper slope eventually contact the bottom, but those carried to oceanic areas only descend to certain depths (depending upon the local temperature structure), never contact the bottom and are permanently lost to the primary population. The young of these species that find the bottom relatively quickly move to the habitat of their size and age group, which tends to be at lesser depths than the adults, because they are undergoing a temperature acclimation from the warm, epipelagic environment to the colder, demersal upper-slope environment. During development and maturation in this demersal habitat, young individuals gradually descend to depths occupied by the reproducing segment of the population. A few individuals wander into even greater depths, where decreased temperatures may slow their growth rate but increase their longevity. These latter individuals are the largest, but least numerous members of the population.

The second hypothesis is that species that change only slightly in mean size with depth, and usually occupy a more restricted bathic range, have demersal eggs and larvae or bear their young alive. The young of these species already inhabit the depths and temperatures occupied by the adult segment of the population. Thus, they do not undergo change from a warm, epipelagic existence to a cold, benthonic existence, and become more restricted in demersal depth ranges while dispersing over the entire bathic range of the population.

Of the 15 species demonstrating a size-depth relation and for which we hypothesize pelagic young, nine are represented by pelagic larvae identifiable to the familial or generic level: Neoscopelidae (implied); *Chlorophthalmus*; and *Chaunax* (Mead, et. al., 1964); Macrouridae (Marshall, 1965); *Antigonia* (Berry, 1959); and *Merluccius* (Bigelow and Schroeder, 1953). Four of the remaining six species (*Synagrops bella, Setarches guentheri, Cyttopsis roseus, Zenion hololepis*) are represented at the familial level by larval specimens taken in epipelagic plankton tows during investigations off southeastern United States by the R/V *Theodore N. Gill.* The families of the two remaining species (*Polymixia lowei* and *Parahollardia schmidti*) have not been recognized in the *Gill* collections, but pelagic berycomorph and plectognath larvae are common (Jack Gehringer and Frederick H. Berry, Bureau of Commercial Fisheries, Biological Laboratory, Brunswick, Georgia, personal communication).

Two of the four species with no size-depth correlation and for which we hypothesize demersal eggs or larvae, are thought to have benthonic young. We assume the scyliorhynid *Galeus arae* to be viviparous (Stewart Springer, personal communication). The deep-sea iniomid fishes, which would include *Bathypterois bigelowi* under consideration here, produce a relatively small number of eggs that develop on or near the bottom (Mead, et al., 1964). The two remaining species, *Xenolepidichthys dahlgleishi* and *Bembrops gobioides*, may be considered as negative evidence supporting the above hypotheses since grammicolepid and percophidid eggs and larvae have not been recognized in the *Gill* epipelagic plankton collections (J. Gehringer and F. Berry, personal communication).

In the slope environment, size-depth relations appear influenced by two factors: vertical movements of population segments of species having planktonic eggs and larvae; and the physiological response of all populations to the direct relations of depth and temperature in slower growth, increased age, and greater maximum size with increased depth.

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APPENDIX I

Depth Distribution of Fish Families and Species in Average Density of Individuals per Hectare

	75	101	151	201	251	301	351	401	451
Depth range (fathoms)	100	150	200	250	300	350	400	450	500
Myxinidae			.02	.02		.10			
Myxine glutinosa			.02	.02		.10			
Scyliorhinidae		1.31	1.21	2.78	3.37	3.13	.08		
Galeus arae			1.05	2.57	2.84	3.03			
Galeus cadenati				.13	.53	.10	.08		
Scyliorhinus hesperius		.11	.05	.08					
Schroederichthys maculatus		1.20	.11						
Squalidae		.17		.34	.05	.55			
Etmopterus bullisi						.36			
E. schultzi				.06	.05	.03			
E. virens				.22		.07			
Centrophorus granulosus				.02					
C. uyato						.03			
Squalus cubensis		.17		.02		.03			
S. blainvilli				.02		.03			
Torpedinidae				.02					
Torpedo nobiliana				.02					
Rajidae		.17	.41	.74	.20	.64	.31	.21	.06
Raja lentigenosa		.17							
R. teevani						.03			
Breviraja colesi						.06			
B. spinosa			.21	.16	.10				
Cruriraja poeyi				.22					
C. rugosa				.18	.10	.52		.21	

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Gen., sp. indeter.			.20	.18		.03	.31		.06
Pseudorajidae			.15	1.33	.24	.23			
Pseudoraja atlantica			.15	1.33	.24	.20			
P. fischeri						.03			
Anacanthobatidae				.46	.19		.31		
Anacanthobatis americanus				.46	.19		.31		
Chimaeridae		.06	.02	.08		.20			
Hydrolagus alberti		.06		.04		.20			
Neoharriotta carri			.02	.04					
Argentinidae	.16	1.15	.99	.85					
Argentina striata		1.15	.51	.85					
Gen., sp. indeter.	.16		.48						
Alepocephalidae							.31	.73	.06
Muraenidae	.05								
Gymnothorax ocellatus	.05								
Congridae	2.14	6.08	.31	.36	.29	.49	1.22	.31	.44
Synaphobranchidae									.13
Synaphobranchus kaupi									.13
Halosauridae				.32	.38	.39	1.37	.20	.38
Notacanthidae							.08		
Notacanthus analis							.08		
Synodidae	13.91	1.66	1.97						
Sudidae			1.57	23.03	15.05	3.42			
Chlorophthalmus agassizi			.71	20.26	14.42	3.42			
Parasudis truculentus			.86	2.77	.63				

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Bathypteroidae					*.48*	*1.76*	*.99*		
Bathypterois bigelowi					.48	1.50	.38		
B. viridensis							.61		
Bathypterois sp.						.26			
Neoscopelidae				*2.34*	*6.06*	*19.14*	*9.40*	*.21*	*.06*
Neoscopelus macrolepidotus				2.34	6.06	19.14	9.40	.21	.06
Ateleopidae			*.07*	*.02*	*.10*	*.03*	*.08*		
Ijimaia antillarum			.07	.02	.10	.03	.08		
Gadidae	*3.23*	*.14*	*.02*	*2.12*	*4.17*	*2.51*			
Macrouridae		*.20*	*3.94*	*18.26*	*21.93*	*12.78*	*9.39*	*.31*	*7.39*
Steindachneria argenteus		.20	.49	2.20	.24	.10			
Coelorhynchus caribbaeus			1.09	.79					
C. carminatus			.90	2.59	4.09	.52			
Nezumia bairdii			1.46	6.30	4.38	8.70	.23	.10	.38
N. hildebrandi				2.22	8.70	1.89	.76		.63
Trachonurus sulcatus						.13	.38	.10	.31
Oxygadus occa							.23		.06
Gadomus longifilis					.14	.36	.38		.75
G. arcuatus							.31	.10	
Bathygadus vaillanti				.04	3.03	.13	.92		1.31
B. favosus									2.63
B. macrops									.44
Hymenocephalus sp.				4.12	1.35	.95	6.18		
Cariburus sp.									.88
Bregmaceriidae				*.04*					

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Bregmaceros atlanticus				.04					
Merluciidae		*.09*	*.05*	*1.58*	*.24*	*1.53*	*.08*		
Merluccius albidus		.09	.05	1.58	.24	1.53	.08		
Fistulariidae	*.05*								
Fistularia tabacaria	.05								
Polymixiidae	*1.09*	*12.74*	*26.23*	*15.47*	*.14*	*.03*			
Polymixia lowei	1.09	12.74	26.23	15.47	.14	.03			
Trachichthyidae	*.05*		*.02*	*.59*		*.03*			
Hoplostethus sp.	.05		.02	.59		.03			
Holocentridae	*.26*	*.03*							
Myripristis jacobus	.26	.03							
Diretmidae				*.02*		*.26*			
Diretmus argenteus				.02		.26			
Zeidae		*3.24*	*51.74*	*73.94*	*1.40*	*.78*			
Zenion hololepis		2.90	50.95	72.40	.87	.62			
Cyttopsis roseus		.20	.54	1.52	.53	.16			
Parazen pacificus		.14	.25						
Zenopsis ocellatus				.02					
Grammicolepidae		*1.15*	*2.85*	*17.32*	*.10*				
Xenolepidichthys dahlgleishi		1.15	2.85	17.32	.10				
Caproidae	*.36*	*41.73*	*26.83*	*.06*					
Antigonia capros	.10	.23							
A. combatia	.26	41.50	26.83	.06					
Bathyclupeidae			*.02*	*3.41*	*1.44*	*1.11*	*.08*		
Bathyclupea argenteus			.02	3.41	1.44	1.11	.08		

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Serranidae	*5.64*	*9.01*							
Serranus phoebe	.89	.03							
Unidentified	4.75	8.98							
Lutjanidae	*7.09*	*.95*							
Lutjanus vivanus	1.30	.03							
Pristipomoides aquilonaris	.68								
Unidentified	5.11								
Priacanthidae	*.26*								
Pseudopriacanthus altus	.21								
Priacanthus arenatus	.05								
Apogonidae	*2.50*	*4.58*	*28.48*	*10.08*	*3.85*	*4.24*			
Synagrops bella	.36	4.38	9.26	7.02	1.97	.75			
Synagrops sp. 1			19.06	.61					
Synagrops sp. 2		.20	.16						
Epigonus pandionus				.65		.49			
Unidentified sp. 1	2.14								
Unidentified sp. 2				1.80	1.88	3.00			
Branchiostegidae	*.42*								
Caulolatilus sp.	.42								
Sciaenidae				*.02*					
Mullidae	*.21*								
Pseudupeneus maculatus	.05								
Unidentified	.16								
Labridae	*.16*								
Percophididae	*.21*	*1.51*	*9.1*	*.79*	*.97*	*.62*			

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Bembrops maculatus		.80	.10	.08					
B. anatirostris		.71	.05						
B. gobioides			.76	.06	.87	.13			
B. magnisquamis				.65	.10	.49			
Bembrops sp.	.21								
Uranoscopidae	2.29	.17	.05						
Kathetostoma cubana	2.29	.17	.05						
Gempylidae	.26	1.09	.62	1.25	.34	.19	.08		
Gempylus serpens				.91	.34	.16			
Epinnula o. americana	.26	1.09	.60	.22					
Unidentified sp.			.02	.12		.03	.08		
Trichiuridae		.03							
Scorpaenidae	7.55	1.87	1.85	4.14	.10	3.26			
Setarches guentheri			1.13	4.08	.10	3.26			
Unidentified sp.	7.55	1.87	.72	.06					
Triglidae	4.32	8.38	.34						
Bellator brachychir	3.80	1.78	.21						
B. militaris	.16	.29							
B. egretta		6.11							
Prionotus stearnsi		.20	.13						
Prionotus sp.	.36								
Peristediidae		.89	.90	4.36	2.31	2.54	.31		
Callionymidae		.03	.15	.04	.05	.07			
Callionymus agassizi		.03	.15	.04	.05	.07			
Brotulidae	.21	.11	.21	.73	.72	1.08	8.16	.52	2.38

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Ophidiidae	*3.18*	*6.37*	*.51*	*.63*		*.07*			
Stromateidae		*.09*	*.02*	*.06*					
Cubiceps nigriargenteus?		.09	.02	.06					
Bothidae	*12.14*	*1.10*	*.11*	*.12*					
Citharichthys cornutus	7.92	.12							
Gastropsetta frontalis	.10								
Cyclopsetta fimbriata	.21								
Chascanopsetta sp.			.03						
Unidentified	3.91	.98	.08	.12					
Pleuronectidae		*2.15*	*2.64*	*2.18*					
Cynoglossidae	*.05*								
Symphurus sp.	.05								
Triacanthodidae	*.31*	*1.67*	*.80*	*1.31*	*.05*	*.46*			
Hollardia hollardi	.31	1.61	.30						
Parahollardia schmidti		.06	.38	1.29	.05	.46			
Johnsonina eriomma			.12	.02					
Tetraodontidae	*.16*								
Sphoeroides sp.	.16								
Batrachoididae	*20.05*	*2.93*							
Porichthys porosissimus	20.05	2.93							
Lophiidae	*.26*	*.11*	*.05*	*.10*		*.06*			
Chaunacidae		*1.71*	*6.18*	*12.00*	*5.43*	*5.35*	*.23*		
Chaunax pictus		1.71	6.18	12.00	5.43	5.35	.23		
Ogcocephalidae	*6.61*	*.29*	*.58*	*2.18*	*1.01*	*3.81*	*.84*	*.10*	
Halieuthichthys aculeatus	4.84	.17							

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Ogcocephalus parvus	1.61	.03	.07						
Ogcocephalus sp.	.16	.06	.08						
Dibranchus atlanticus		.03	.43	2.18	1.01	3.81	.84	.10	

ECOLOGICAL EFFICIENCY OF A PELAGIC MYSID SHRIMP; ESTIMATES FROM GROWTH, ENERGY BUDGET, AND MORTALITY STUDIES[1]

Robert I. Clutter[2] and Gail H. Theilacker[3]

ABSTRACT

The net ecological efficiency (yield/assimilated) of a population of *Metamysidopsis elongata* (Crustacea, Mysidacea) is estimated to be 32 %. The gross ecological efficiency (yield/ingested) is probably between 19 % and 29 %.

Energy use by the field population was calculated from estimates of age specific natural mortality rates and data on growth, molting, reproduction, and respiration. Average growth and molting rates were determined by rearing the mysids in the laboratory. Size specific fecundity was determined from field and laboratory observations. The calorie contents of the mysids, their molts, eggs and larvae were estimated by bomb calorimetry and in part from biochemical composition. The energy used in metabolism was calculated from size specific respiration and data on body composition.

Biological systems are organized by the flow of energy. Trophic structure, numbers of steps in food chains, and numbers of conjunctions in food webs depend on the amount of energy passed through populations to other populations. Energy units provide a means of expressing productivity in terms common to all organisms.

The energy produced in the breakdown of biomass by organisms is stored as chemical energy in the pyrophosphate bonds of adenosine triphosphate (Morowitz, 1968). The overall thermodynamic efficiency of this process is similar in all animals, about 60 to 70 % according to Krebs and Kornberg (1957). It has been suggested (e.g. Slobodkin, 1961, 1962) that the efficiency of energy transfer between populations of animals is also fairly constant. This efficiency is necessarily of lower order because, for example, there are losses involved in synthesizing macromolecules, in continually resynthesizing proteins that undergo thermal denaturation, in transforming foodstuff energy into work energy (about 65 % efficiency), and in the degradation of energy during the performance of work. All energy that passes through a population is either lost as heat or passes on to another trophic level. If one assumes that all mortality is caused by predation, the gross ecological efficiency (Phillipson, 1966) of energy transfer through that population is the ratio of the energy yield in mortality to the energy ingested.

Through laboratory studies of growth, molting, reproduction, respiration, body composition, and energy content, we have constructed an energy budget for the pelagic mysid shrimp *Metamysidopsis elongata* (Holmes). Various aspects of the distribution, behavior, and population biology of this species have been described by Clutter (1967, 1969) and Fager and Clutter (1968). The energy budget data, together with estimates of natural population mortality rates, are used to estimate net and gross ecological efficiencies for the field population.

GROWTH AND DEVELOPMENT

Metamysidopsis elongata is a member of the Mysidae, a family that is ubiquitous and often very abundant in most of the neritic zones of the world ocean. This species is free-swimming and occurs in shoals and swarms just above the sand bottom in areas where surf is common

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(Clutter 1967, 1969).

As is characteristic of mysids, the eggs and larvae are held by the oostegites (brood pouch) of the adult females until they develop into juveniles that are similar in form to the adults. The juveniles grow by shedding their exoskeletons (ecdysis) at intervals that become progressively longer until they reach maturity. Males and females develop distinguishable morphological features during the period of rapid growth prior to maturity. Growth becomes progressively slower after maturity. Although there is no evidence that death occurs because of physiological aging, the maximum age observed was about 9 months. Most animals survive less than 3 months in the natural environment . We assume that most of the natural mortality is caused by predation, especially by fishes.

Some growth experiments have been reported for other species of Mysidae. Blegvad (1922) determined the growth rates of a few individuals of *Mysis inermis* from first stage juveniles through early maturity. Nouvel and Nouvel (1939) made disjunct determinations of time between molt stages for some size groups of *Praunus flexuosis*. Nair (1939) observed the time sequence in the egg and larva development of *Mesopodopsis orientalis*, determined the size and age at liberation, and noted the size at sexual maturity of males and females. In his review of growth in some marine Crustacea, Kurata (1960) presented the results of growth studies made by Ishikawa and Oshima on *Neomysis japonica* and by Matsudaira et al. on *Gastrosaccus vulgaris*. Mauchline (1967) maintained adult *Schistomysis spiritus* in the laboratory, estimated the time they take to attain sexual maturity, and estimated the minimum incubation time. Considering differences between species, sizes, and environmental temperatures, these reported patterns of development and size increase per molt are compatible with the results of our study.

CULTURE METHODS

Experimental animals were collected during the day from the middle of their habitat with nets (Clutter, 1965; Fager, Flechsig, Ford, Clutter, and Ghelardi, 1966). They were placed in large (20-50 liter), opaque plastic containers with covers and transported to the laboratory within 1 to 2 hr after the time of capture.

The culture methods were about the same as those described by Lasker and Theilacker (1965) for euphausid shrimps. Individual animals were placed in rectangular clear plastic containers in about 500 ml of sea water. The small containers were partly immersed in trays of running sea water. Since the running sea water was pumped continuously into the aquarium from midwater offshore, within the *Metamysidopsis* habitation zone, the laboratory temperatures (14°-20° C) were about the same as those that the animals would have experienced in their natural environment.

Animals of both sexes and of several sizes were selected for the experiments. Young juveniles were procured by placing pregnant females in containers and recovering the young on the day following their release from the brood pouch, which occurred at night. These young were then placed in separate containers. To determine the incubation time, i.e. the time from fertilization of the eggs to release from the brood pouch as juveniles, pregnant females with known times of fertilization were placed in individual containers so that larval development could be observed.

Mysids of all ages were fed freshly hatched nauplius larvae of brine shrimp, (*Artemia salina*). Twice each week the mysids were removed while their containers were emptied of excess food and cleaned with hot fresh water followed by a sea water rinse. They were then provided with excess quantities of fresh nauplii in clean sea water.

The containers were examined every day for the presence of molts or, occasionally, carcasses. The molts and carcasses were removed and placed individually in small vials of 5 % Formalin for subsequent microscopical examination and measurement.

OOGENESIS AND INCUBATION

Since *Metamysidopsis* has a transparent carapace and body wall, it is possible to observe the late stages of oogenesis in live animals without dissecting them. The ovary (cf. Nair, 1939, for description) is situated in the interspace between the alimentary canal and the pericardial floor. Its most obvious feature is the pair of larger tubes that lay side by side. It is in these tubes that the eggs to be extruded into the brood pouch are invested with yolk. The process of yolk formation takes about a week in *Metamysidopsis* and is completed just before the female molts and copulates. By observing the ova in these tubes it is possible to estimate the size or age at first reproduction in maturing females, and to count the number of eggs that will be spawned by reproducing females of all ages.

Copulation occurs at night within 2 to 3 min after the mature female molts, during which time sperm are passed into the empty brood pouch by the attending adult male. The eggs are subsequently extruded into the brood pouch where they are fertilized. The eggs hatch from the vitelline membrane after 2 to 3 days. According to Manton (1928) and Nair (1939) a larval ecdysis occurs in the brood pouch shortly before the larvae are liberated. These late stage larvae have movable appendages and pigmented eyes that show through the transparent oostegites of the brooding female. The small quantity of yolk that is present after the larval ecdysis is absorbed, or nearly so, prior to liberation from the brood pouch.

After liberation the larvae tend to sink, then, according to Nair (1939), they undergo a second larval ecdysis after which the statocysts appear and they are capable of swimming. The mysids assume this highly mobile juvenile form within a few minutes after liberation. Although we did not attempt to distinguish sexes of larvae and juveniles, the observations of Nair (1939) indicate that dimorphism is exhibited by the antennules and abdominal appendages even though neither the brood pouch nor the penis is developed.

Incubation time was determined in the laboratory. Adult females and adult males were observed in an aquarium during molting and copulation. Ten females were caught after being observed *in copulo* and were placed in separate containers of sea water at the temperature of their natural environment at that time (17°-19° C). Five of them were removed, at various times, to determine the stages of development of the young. The remaining five all released their young as juveniles on the tenth day after fertilization.

In addition, a large number of nonpregnant adult females were kept in separate containers for various periods up to 157 days. The range of intermolt periods in 218 observations was 5 to 13 days; the median and modal values were both 10 days. There was no obvious temperature effect. The adult females molt just before fertilization and just after liberation of the young; therefore, the average incubation time was taken to be 10 days. This is intermediate between incubation times given for Mysidae that live and reproduce at higher and lower temperatures. Nair (1939) determined the incubation time of *Mesopodopsis orientalis* to be 4 days at 25° to 29° C. Mauchline (1967) reports a minimum incubation time of 3 weeks for *Schistomysis spiritus* at 12.5° C.

MOLTING

To avoid handling and possible injury of the experimental animals, the growth rates were determined by measuring molts. The molts suffered no appreciable decomposition because they were collected on the day following ecdysis. The morphological development of the animals was usually discernable from their molts. But the molts are fragile, split just back of the carapace where the animals emerge, and easily stretched out of shape. Therefore, to measure growth it was necessary to measure a part of the molt that always retained its form and bore a consistent relationship to the body length.

Uropod-Body Length Relationship

The exopod of the uropod (tail fan) was used to estimate the body length of each animal for its previous intermolt period. The uropods were measured from the base (end of last abdominal segment) to the tip, not including spines, which were sometimes broken, with an ocular micrometer, at 27.5 × magnification.

The relationship between uropod length and body length was established from a selected series of 94 animals that had been collected in the field and preserved. The series included animals that ranged in body length from 0.8 mm to 7.2 mm, and included late stage larvae, juveniles, immatures, and adults. Both sexes were included; there was no difference between sexes in this relationship.

The body length was measured from the end of the last abdominal segment (base of uropod) to the anterior edge of the carapace, behind the insertion of the eyestalk. Mysids tend to curl when preserved, and they can be distorted to appear longer if they are stretched when measured. To avoid this we chose specimens that were at most only slightly curved, and measured the length of the arc through the midline of those that had significant curvature, rather than the straight line distance between head and tail.

As shown in Figure 1, the relationship between uropod length and body length is linear. The body length is 4.5 times the uropod length.

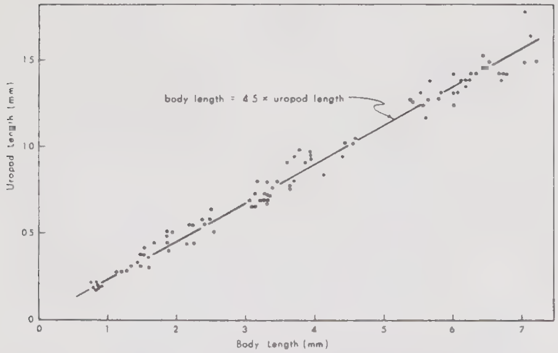

FIGURE 1.—Relationship between uropod length and body length of *Metamysidopsis*.

Molting Frequency

Average intermolt periods were estimated from 414 observations, 146 on males and 268 on females. In many cases several observations were made on the same animal. The maximum period of laboratory survival for a single animal was 157 days, and the maximum number of molts observed for a single animal (not the same animal) was 21. The molting frequency data for animals reared in the laboratory are summarized in Table 1. The sex of the juveniles was established after they had grown large enough to develop obvious morphological differences.

TABLE 1.—Frequency of molting periods observed for *Metamysidopsis* in the laboratory.

	Sex and length	Intermolt Period (days)													
		3	4	5	6	7	8	9	10	11	12	13	Mode	Median	Mean
	Females														
Body length (mm)	2		8										4	4	4.0
	3		6	2									4	4	4.3
	4		5	3	1								4	4-5	4.6
	5		3	7	7	1	5	2					5-6	6	6.2
	6			10	7	9	13	13	28	17	5	8	10	9-10	9.2
	7			11	8	6	9	16	12	28	9	9	11	10	9.4
	Males														
Body length (mm)	2	11											3	3	3.0
	3	2	11	1									4	4	3.9
	4	2	15	8	1	1							4	4	4.4
	5		6	29	20	4							5	5-6	5.4
	6		6	11	8	7	3						5	5-6	5.7

Supplementary data on molting frequency in the field population were obtained indirectly. Over a period of 3 days, 1,211 juveniles + immatures and 2,979 adults were brought into the laboratory late in the day and placed in large aquaria. The following morning all the animals and their molts were collected and counted. Of the juveniles + immatures 218 or 18 % had molted, and of the adults 356 or 12 % had molted. The reciprocal of the relative number molting is an estimate of molting period. The observed reciprocals were 5.6 for juveniles + immatures and 8.3 for adults. Since these values are midway in the ranges shown by laboratory animals (3-8 days for juveniles + immatures and 4-13 days for adults) we assume that the laboratory observations are valid estimates of molting frequency in the population as a whole.

Although our observations were made from February to October, and the water temperatures in the rearing troughs varied from 14° to 20° C, we were unable to detect any obvious effects of temperature or time of year on molting frequency or growth rates. Nouvel and Nouvel (1939) stated that the intermolt period for *Praunus flexuosis* is least during the warmest months, and the incubatory period is 15 days in August and 3 to 4 weeks in September. Lasker (1966) showed that *Euphausia pacifica* intermolt periods varied as the water temperature fluctuated, and that the intermolt period was shortened by an artificially produced warm period, but that temperatures above 12° C did not accelerate molting further.

Since we do not have evidence to the contrary, we must assume that our laboratory observations on molting frequency provide adequate average values. From the median values given in Table 1 and estimated average growth rates (see below) we have estimated the molting schedules of females and males from juveniles to mature adults as follows:

Females: first six molts — 4 days
seventh molt — 5 days
eighth molt — 6 days
ninth molt — 8 days
tenth molt and thereafter — 10 days

Males: first four molts — 3 days
fifth to eighth molts — 4 days
ninth and tenth molts — 5 days
eleventh molt and thereafter — 6 days

GROWTH AND MATURATION

Evidence of the temporal sequence of growth and maturation can be obtained from following peaks of abundance of size groups in natural populations. We sequentially sampled the mysids in the field and observed some shifting peaks. But we consider that the results are not very reliable because of temporal changes in age-specific mortality rates (Fager and Clutter, 1968). Therefore, all the age-specific growth estimates presented here were obtained from laboratory studies.

Observed Growth

A few mysids were reared in the laboratory from fertilized egg to adult. Several were reared from egg through the juvenile stage. In addition, larger numbers of various sizes were collected in the field and kept in the laboratory for several molts.

The growth data from these animals were combined as shown in Figure 2 (females) and Figure 3 (males). The sexes were separated because the growth and molting rates of males and females are different. As they are shown in Figures 2 and 3, these individual growth curves are simplified and slightly incorrect representations of true growth, for two reasons. First, the growth of the body integument is represented to be continuous, whereas it actually occurs in discrete increments. Second, the age

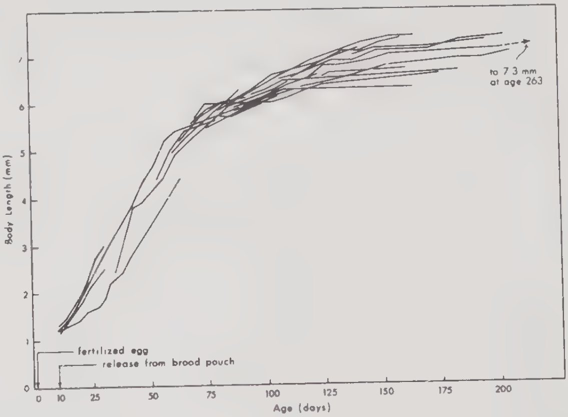

FIGURE 2.—Observed growth in length (from molts) of *Metamysidopsis* females in the laboratory.

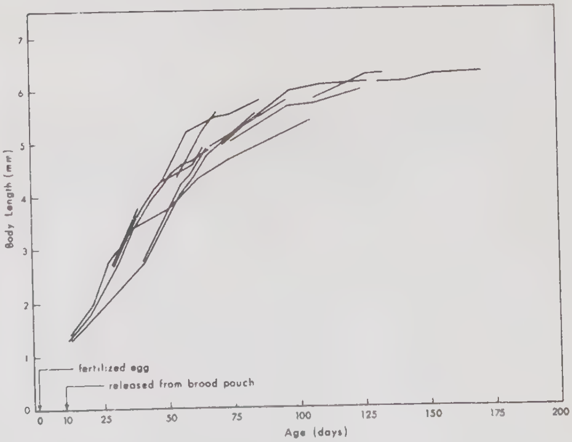

FIGURE 3.—Observed growth in length (from molts) of *Metamysidopsis* males in the laboratory.

shown is the age of the animal at the time it molted, rather than the age at the time that the molted integument was first formed. The procedure for combining the various growth curves of individual animals was to first plot the growth of the animals of known age, and then plot the other growth curves (actual ages unknown) in a manner that showed the least variation from the apparent trend.

Some of the apparent variability in growth rates may be attributable to differences in the temperature at which the growth occurred, but we did not detect any obvious temperature effect. Considerable individual variability occurred among animals of the same size or age that were reared simultaneously.

Maturation

Changes in morphology in relation to size, and known or estimated age, were observed in the molts of animals reared in the laboratory. Observations were made on live females collected from the field population to determine the size at which yolk invested ova first appear in the ovaries. Supplementary observations on the relationship between size and body form were made on preserved animals that had been collected in the field. There is some evidence from previous samples taken for other purposes (Clutter, 1967, 1969) that the relationship between size and stage of development may vary seasonally. But during the period of observations reported here, this did not appear to be significant.

In particular, we wished to determine (1) the size (and subsequently the age) at which males and females were easily distinguishable by their secondary sexual characteristics, (2) the size at the onset of maturity, and (3) the size at which spawning and brooding of eggs and larvae occurs. The external characteristics that most obviously separate males from females of this species are the enlarged oostegites (brood pouches) of the females and the enlarged pleopods (abdominal legs) and antennae of the males.

There is some variability in the size at which the stages of development occur. Therefore, our estimates are average values. The larvae are released and juvenile form is attained at age 10 days; at this time both sexes are about 1.2 mm long (body length; excluding antennae, eyes, and tail fan). Males exhibit sub-adult morphology when about 3.7 mm long, and become mature at 4.3 mm. Females exhibit subadult form at 4.0 mm, the ova become infused with yolk at 4.5 mm, and the eggs are extruded into the brood pouch, fertilized, and incubated at slightly less than 5.2 mm.

Average Growth in Length

Average continuous growth curves were fitted by eye to the combined growth data plotted in Figures 2 and 3. These curves are represented by the lower curves (fine, continuous unbroken lines) in Figure 4 (females) and Figure 5 (males). These continuous curves represent the size of the molt at the time—days from fertilization—that the molt was shed. Actually the integument of the animal had attained that size by the beginning of the intermolt period in question. The true growth of the integument of the average animal is represented by the stairstep pattern, which is based on the molting frequency analysis. The broken curved line of continuous growth (Fig. 4 and 5) represents the probable pattern of temporal change in average organic weight of the animal. This curve connects the points halfway between the beginnings and endings of the intermolt periods.

Since the average sizes at various stages of development were determined, it was possible to estimate the average time schedules of maturation and reproduction for females and males on the basis of the growth curves. The average female begins to develop a brood pouch at the seventh molt, 39 days after becoming a fertilized egg. Yolk invested ova begin to be formed at 45 days, during the ninth intermolt period; the ova are extruded into the developed brood pouch and fertilized at the beginning of the tenth intermolt period, at 53 days; and reproduction can occur at 10 day intervals thereafter.

Males and females grow at rates that are indistinguishable up to the age of about 30 days, even though the juvenile males molt more frequently than juvenile females. After that the

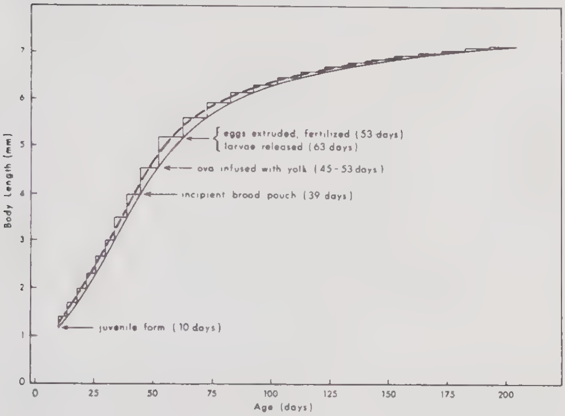

FIGURE 4.—Average growth in length of female *Metamysidopsis* in the laboratory. The lower curve (fine continuous line) was fitted to molt size data (Fig. 2). The steps represent changes in integument size. The upper curve (heavy broken line) represents the average size of the animals, assuming that the addition of body tissue is continuous.

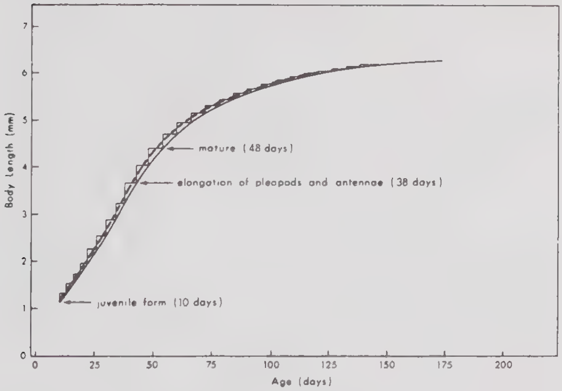

FIGURE 5.—Average growth in length of male *Metamysidopsis* in the laboratory. The lower curve (fine continuous line) was fitted to molt size data (Fig. 3). The steps represent changes in integument size. The upper curve (heavy broken line) represents the average size of the animals, assuming that the addition of body tissue is continuous.

males grow more slowly. The males develop easily recognized secondary sexual characteristics at an average age of 38 days and become sexually mature after about 48 days. Average age at maturity was estimated from observations of testes and copulatory behavior in the laboratory as well as from external morphology.

Average Growth in Weight

To estimate growth in terms of energy it is necessary to translate growth in length into growth in dry weight. This growth in dry weight is then translated into growth in organic (ash-free) weight and thereafter into calories.

The dry weights of *Metamysidopsis* of body lengths ranging from 1.9 mm to 6.5 mm were determined. The animals were captured alive, measured, washed very briefly with distilled water, and dried at 60° C in an oven for 24 hr. They were then weighed individually on a Cahn electrobalance immediately after they were removed from the oven.

The observed relationship between body length and dry weight is shown in Figure 6.

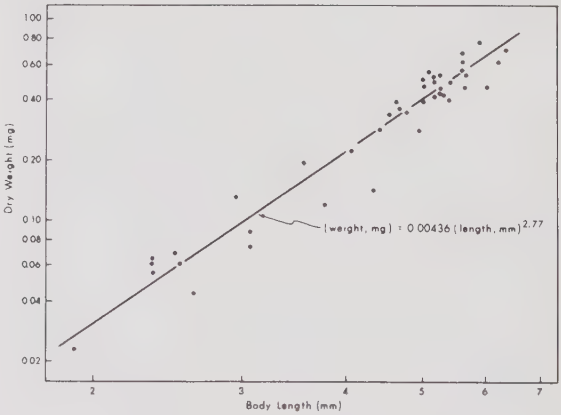

FIGURE 6.—Relationship between body length and dry weight of *Metamysidopsis*.

The equation for the relationship was determined empirically by fitting a straight line to the logarithms of body length and dry weight by the method of Bartlett (1949). The relationship is:

$$\log_e (\text{weight}) = -5.436 + 2.77 \log_e (\text{length})$$

or

$$\text{weight} = 0.00436 (\text{length})^{2.77}$$

where weight is expressed in mg and length in mm.

It is common to assume that body weight and body volume have a linear relationship, and that body volume is proportional to the third power of length. Therefore dry weight is expected to be proportional to the third power of body length (Bertalanffy, 1951). The observed relationship does not quite conform to the expected. The relationship between body length and body diameter appears to be linear (Fig. 7); therefore the body volume must be proportional to the third power of the body length. The observed relationship between weight and length could be the result of orthogonal growth of the appendages, which become progressively larger as the animals mature.

From the average length-weight relationship and the average continuous growth in length curves (Fig. 4 and 5) we have calculated the average growth in weight curves shown in Figure 8. The average continuous growth in length curves represented by the heavy broken lines in Figures 4 and 5 were used to calculate growth in weight, because we assume that growth in organic weight is continuous during intermolt periods even though growth of the integument occurs in discrete steps. The estimated growth in weight of males was extrapolated by eye from age 175 days to age 204 days. We do not have laboratory growth estimates for these larger males, but they occurred in the field population.

The average dry weight per egg (140 eggs in sample) was 5.5 μg. Larvae weigh slightly less than this because they lose weight through metabolism while in the brood pouch, even though their ash content is slightly higher than that of the eggs.

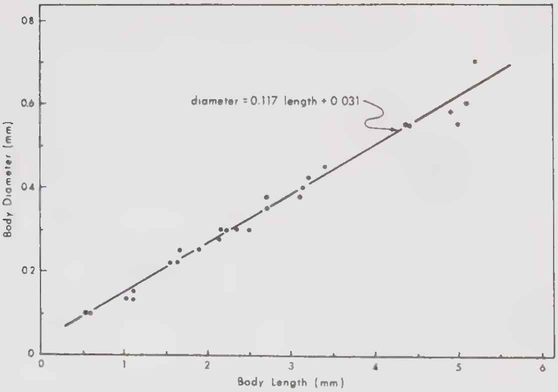

FIGURE 7.—Relationship between body length and body diameter of *Metamysidopsis.*

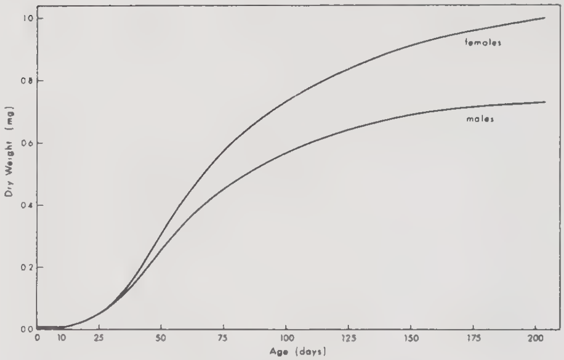

FIGURE 8.—Average growth in dry weight of *Metamydisopsis* females and males in the laboratory.

REPRODUCTION

Data on reproduction and associated energy use are easier to obtain for Mysidae than for most pelagic invertebrates. The eggs and larvae are carried in the brood pouch of the female, and the incipient eggs can be counted prior to their full development and extrusion because the body walls of the mysids are transparent. In addition, copulation and fertilization can be observed in the laboratory, and frequency of pregnancy among mature females can be observed in the natural population through sequential sampling because all stages live in the same area while gestating as they do when not reproducing. Nevertheless, average reproduction rate in these animals is not easy to assess with absolute certainty.

FECUNDITY

Minimum Estimate

The most straightforward way to estimate fecundity is to collect animals in the field, preserve them, and count the number of eggs or larvae carried by females of different sizes. Figure 9 shows the relationship between body lengths and number of young for 310 females collected in the field at various times during the year. The data include 125 females bearing eggs and 185 bearing larvae; we excluded animals that had obviously lost young during capture and preservation. For both eggs and lar-

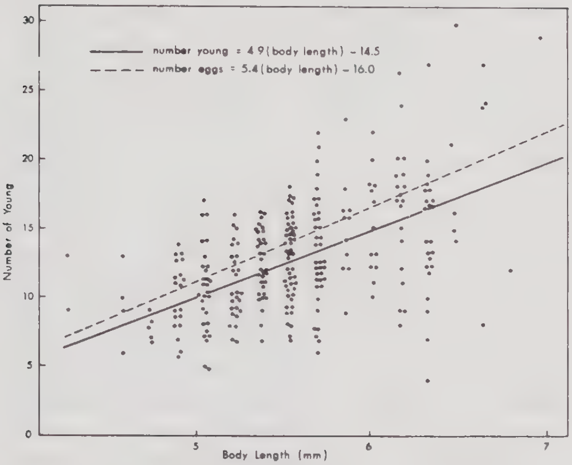

FIGURE 9.—Relationship between body length and number of brood pouch young (eggs and larvae) of preserved animals that were collected in the field. The lower line (continuous) was fitted to the points by the method of Bartlett (1949). The upper line (dashed) represents the equivalent relationship for newly laid eggs, assuming a brood pouch mortality of 0.013/day (see text).

vae, the number of young per female is highly variable. The average relationship between the size of the female and the number of young, calculated by the method of Bartlett (1949), is represented by the straight line: number of young = 4.9 (body length, mm) – 14.5.

This estimate of fecundity is not quite correct because it was made from counts of eggs and larvae that were a few days old. Some eggs and larvae apparently are lost from the brood pouch during the incubation period. Therefore, we adjusted the relationship to account for the mortality which occurs during the incubation period. To estimate the mortality during incubation, counts were made of the maturing ova in the ovaries of 40 adult females and counts were made of late stage larvae in the brood pouches of 27 females of the same size, collected at the same time. The ratio of mean number of larvae/mean number of ova was 0.90. The larvae were estimated to be 8 days old, giving an instantaneous mortality rate of 0.013/day.

The average age of the eggs and larvae from the 310 preserved females (Fig. 9) was estimated to be 7 days. Therefore, the relative survival of the young in the brood pouch between the time of extrusion of the eggs and the estimated average age at which they were counted (7 days) was estimated to be about 0.91. The number of brood pouch young per female was adjusted to the equivalent number of eggs extruded per female by multiplying the number of young by 1/0.91 = 1.10. The relationship (Fig. 9) then becomes: number of eggs = 5.4 (body length, mm) – 16.0, which is shown in Figure 9 as the upper, dashed line.

We consider this to be a minimum estimate of fecundity, because some females that had lost eggs and larvae from the brood pouches during collection and preservation were probably included, despite our attempt to exclude them.

Maximum Estimate

We observed that the females that had released young during the laboratory experiments had a higher apparent fecundity than those that were collected and preserved in the field. It is possible that there was some bias in selecting animals for the laboratory experiments, but we were not aware of any. The number of young released per female is plotted against the body length of the female for those 17 specimens in Figure 10. The average relationship between

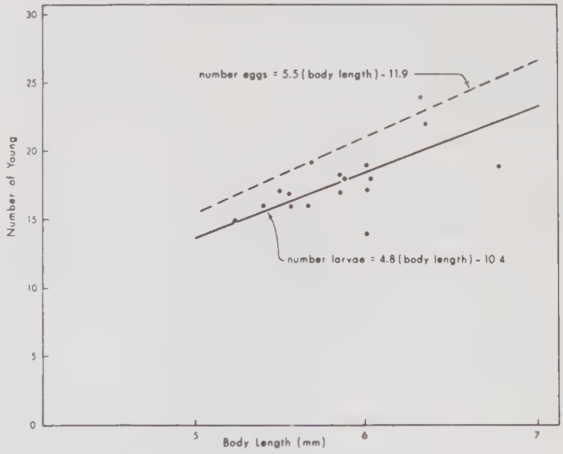

FIGURE 10.—Relationship between body length and number of young released by experimental animals in the laboratory. The lower line (continuous) was fitted to the points by the method of Bartlett (1949). The upper line (dashed) represents the equivalent relationship for newly laid eggs, assuming a brood pouch mortality of 0.013/day (see text).

body length and number of young, calculated by the method of Bartlett (1949), was: number of young = 4.8 (body length, mm) − 10.4. This is represented by the lower, unbroken straight line in Figure 10.

This relationship gives estimates of fecundity that are about 1.5 to 2 young per female higher than the relationship calculated from preserved animals. But this is not quite a maximum estimate of fecundity because it does not include the reduction from mortality that occurs during incubation.

As already demonstrated, we can assume a brood pouch mortality rate of 0.013 per day. The relative survival of young in the brood pouch during the 10 days between the extrusion of eggs and the release of larvae was therefore estimated to be 0.87. The number of young released per female was adjusted to the equivalent number of eggs extruded per female by multiplying the number of young by 1/0.87 = 1.15. The relationship (Fig. 10) then becomes: number of eggs = 5.5 (body length, mm) − 11.9, which is shown in Figure 10, as the upper, dashed line.

This relationship gives estimates of fecundity that are about four eggs per female higher than the minimum estimates calculated from preserved animals. We consider this to be the maximum estimate of fecundity. It is the same as that used by Fager and Clutter (1968).

COPULATION AND FERTILITY

The fecundity estimates given above apply only to the females that engage in copulation and are fertilized. Mature females that are not fertilized apparently extrude some eggs, but only about one-half the usual number.

Many observations of copulation were made in the laboratory (Clutter, 1969). It occurs in artificial light as well as in the dark, but only at night, between about 2000 and 2400 hr. It occurs within only 2 to 3 min after the mature females molt, and apparently only when the female exudes a pheromone to attract adult males of the same species.

Ten females were captured immediately after they were observed *in copulo* and kept in separate chambers for 10 days. Impregnation had been successful and the usual number of eggs were extruded in every instance. Some adult females that molt do not stimulate males to attend them. Ten adult females were captured after they had been observed to be unattended by males during molting and recovery. They later extruded only about one-half of the normal number of eggs, which eventually disappeared from the brood pouch, presumably because they were infertile. Therefore, the unfertilized females expended only about half the amount of energy in eggs that the fertilized females expended.

Since the mature females are subject to fertilization for only a few minutes following molting, and they apparently do not always attract males during the time, copulation does not always occur. Therefore, not all produce young every 10 days. In a large number of field collections during all seasons, the observed fraction of mature females carrying eggs or larvae in their brood pouches varied from 18 % to 78 %; the mean was 51 %. We are not certain of the source of this variability; there is some evidence that it could be related to population density (Clutter, 1969). We have assumed an average value of 50 % for the purpose of calculating the amount of energy used in reproduction.

On the average, mature females extrude the usual number of eggs about one-half of the time, and they otherwise extrude only one-half of the usual number of eggs. Therefore, the effective average fecundity, in terms of energy used in reproduction (but not in terms of the number of viable young produced), is 0.5 + (0.5) (0.5) = 75 % of the fecundity estimated from counts of young produced/female. For the purpose of calculating the amount of energy used in reproduction the fecundity equations are:

minimum — number of eggs = 4.1 (body length, mm) − 12.0

maximum — number of eggs = 4.1 (body length, mm) − 8.9

The second of these relationships is used in the ensuing energy budget calculations.

RESPIRATION

A polarographic oxygen electrode (Kanwisher, 1959) was used in a closed system to measure the respiration rates of *Metamysidopsis.* Both temperature and oxygen were recorded continuously on a strip chart.

The experimental animals were taken from large constant-flow holding tanks (temperature 14°-17° C) and acclimated overnight at the temperature used in the experiments (13.8°-18.1° C), to avoid the overshoot in oxygen consumption described by Grainger (1956). They were then washed in millipore-filtered seawater, counted, and transferred to previously filtered seawater in the oxygen electrode system. In each experiment an attempt was made to use animals of a limited size range. During the run they were held within a 10-ml chamber, baffled at each end with silk screen cloth of 282 μ mesh aperture size. The water in the closed system circulated through this chamber and then past the electrode at a constant rate. The whole system was immersed in a temperature-controlled water bath.

Oxygen use by bacteria was measured by making blank runs with the same water both before and after each test run. Bacterial use amounted to less than 2 %. Oxygen consumption by the mysids was corrected for bacterial uptake. The decrease in relative oxygen tension with time was nearly linear in both the blank runs and the test runs.

The results of the respiration experiments are shown in Table 2. Observed weight-specific respiration rates (μl O_2/mg dry weight hr) were corrected for the initial percent oxygen saturation and for temperature. In correcting for temperature, a Q_{10} of 1.9 was used (Grainger, 1956). All values were corrected to 16° C, which is about the median of the year-round temperatures that occur in the natural environment of the mysids.

TABLE 2.—Summary of respiration experiments on *Metamysidopsis.*

Specimens	Number	Mean dry weight	Water temperature	Weight-specific respiration rate	
				Uncorrected	Corrected[1]
		Mg.	*° C*	*(µl O₂/mg dry wt hr)*	
Juveniles	99	0.03	13.8	7.71	7.54
Juvenile and immature males and females	176	0.07	18.0	5.40	4.76
"	297	0.08	18.1	5.08	4.48
"	297	0.08	18.1	6.78	5.93
"	132	0.14	13.8	3.92	3.82
Immature females	85	0.28	15.2	1.95	2.46
Males	51	0.31	13.8	3.60	3.53
Brooding females	27	0.47	13.8	3.22	3.16
"	27	0.66	13.8	2.65	2.59

[1] Corrected for oxygen saturation level and corrected to temperature of 16.0° C by using Q_{10} = 1.9 (Grainger, 1956).

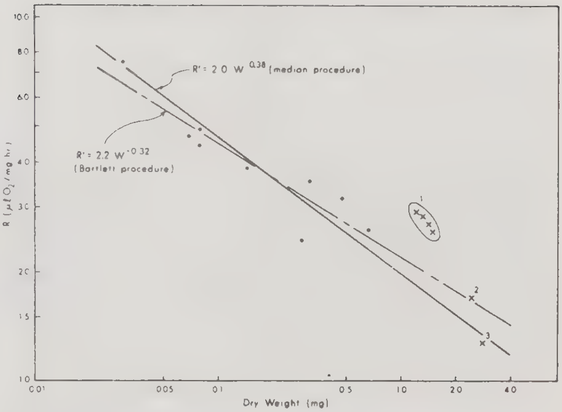

FIGURE 11.—Relation between respiration rate of *Metamysidopsis* and size at 16° C. The symbol *R'* represents respiration rate per dry unit weight (*R/W*). The lines were fitted to the circle points by two statistical pocedures. The *x* points are values calculated from published data on other species of Mysidae: 1-*Neomysis americana* (Raymont and Conover 1961); 2-*Neomysis integer* (Raymont, Austin and Linford 1966); 3-*Hemimysis labornae* (Grainger 1956).

The corrected weight-specific respiration data are plotted in Figure 11 on log-log scales. The symbol *R'* (Conover, 1960) represents the respiration rate per unit dry weight (*R/W*). The average relationship between mean dry weight and *R'* was estimated by two statistical procedures. First, a straight line was fitted to the logarithmically transformed data by the median procedure (Tate and Clelland, 1957). This gave the relationship:

$$R' = 2.0\ W^{-0.38}$$

or

$$R = 2.0\ W^{0.62}$$

where R = respiration rate in μl O_2/hr
and W = mean dry weight in mg.

Second, a straight line was fitted to the logarithmically transformed data by the method of

Bartlett (1949). This gave the relationship:

$$R' = 2.2\ W^{-0.32}$$

or

$$R = 2.2\ W^{0.68}$$

Theoretically, the respiration rate is expected to be proportional to the $^2/_3$ power of weight. Since our estimates are slightly above (0.68) and slightly below (0.62) the expected value of 0.67, we consider that the $^2/_3$ power relationship is the best estimate for *Metamysidopsis* and that the best estimate of respiration rate (μl O_2/hr) is given by the equation:

$$R = 2.1\ W^{0.67}$$

Estimates of weight-specific respiration for three other, somewhat larger, species of Mysidae are compared with *Metamysidopsis* in Figure 11. The upper four points ("1" on Fig. 11) represents results for *Neomysis americana* from Raymont and Conover (1961) that were adjusted from 4° C or 10° C to 16° C by using a Q_{10} value of 1.6 that was estimated from their data. The intermediate point is an estimate of the median value oxygen consumption rate calculated from 12 determinations on *Neomysis integer* (Raymont, Austin, and Linford, 1966) that had been adjusted to 16° C by using a Q_{10} of 1.9 (Grainger, 1956). The lower point was estimated from the results of Grainger (1956) for *Hemimysis lamornae*. The ranges of values for these three larger species are about the same as the range (1-3 μl/hr) calculated from the seasonal change data of Raymont et al. (1966) that had been adjusted to 16° C. The estimates for *Metamysidopsis* and the other three Mysidae all lie well above the relationships calculated for marine planktonic Crustacea by Conover (1960).

BODY COMPOSITION AND ENERGY CONTENT

To estimate the amounts of energy used in respiration, molting, and reproduction it was necessary to determine the body composition of the mysids, their molts, and their young. For these analyses the animals were captured alive and, within 2 hr, placed in a constant-flow holding tank at 15° to 17° C where they were kept for a short time prior to analysis.

BODY COMPOSITION

The estimates of body composition of dried animals and molts are summarized in Table 3. The estimates for ash, protein, lipid, carbohydrate, and chitin are not considered to be accurate past the first decimal point. The fractional percentage values are entered so that the sums will equal 100 %. The methods by which these values were determined will be explained item by item.

To determine dry weights, the animals were washed very briefly with distilled water while still alive, then were oven-dried to constant weight at 60° C. Materials that were available only in small quantities were weighed on a Cahn electrobalance.

Ash

Ash content was estimated by incinerating

TABLE 3.—Average composition and energy content of dry *Metamysidopsis* bodies, molts, eggs, and larvae. Tabulated values for composition are %, and for energy content are cal/mg. The sums of % ash, "protein", lipid, carbohydrate and chitin = 100 %.

	Nitrogen	Carbon	Ash	"Protein"[1]	Lipid	Carbohydrate	Chitin	Energy
	%	%	%	%	%	%	%	*Cal/mg*
Body, whole	11.5	36.8	12.5	69.0	10.0	1.5	7.0	4.60
Body, organic	13.2	42.0	0	79.0	11.4	1.6	8.0	5.24
Molt, whole	--	23.5	44.8	30.9	0	0	24.3	2.48
Molt, organic	--	42.5	0	56.0	0	0	44.0	4.49
Egg, whole	--	58.0	6.0	35.2	58.8	0	0	7.16
Egg, organic	--	61.8	0	37.5	62.5	0	0	7.62
Larva, whole	--	45.7	6.6	60.8	28.9	0	3.7	5.78
Larva, organic	--	48.8	0	65.0	31.0	0	4.0	6.20

[1] "Protein" may include free amino acids.

whole animals or molts in a muffle furnace at 500° C and weighing the residue. Ash determinations were made on six samples composed of mixed animals, juveniles, immatures, adult males, and adult females. The samples contained from 2.7 to 7.3 mg of dried animals; the mean ash content was 12.5 % of the dry weight, and the range was 9.4 to 13.3 %. There was no obvious difference between age groups or sexes. This ash content is within the range, but slightly higher than the mean, of values reported for other Mysidae: *Mysis flexuosa* — 16 % (Hensen, 1887) and 11.9 % (Delff, 1912, quoted by Vinogradov, 1953); *Neomysis integer* — 7.9 % (Raymont, Austin, and Linford, 1964); *Siriella aequiremis* — 10.2 % (Omori, 1969).

Molts used for ash determinations were collected in the laboratory immediately after they were shed. Two samples, weighing 1.1 and 0.6 mg, composed of molts from a wide size range of mysids of both sexes had ash contents of 44.4 % and 45.7 %; the mean was 44.8 %. Lasker (1966) reported a similar value (46 %) for *Euphausia pacifica*. This high ash content in the molts suggests that a large fraction of the total body ash resides in the integuments of the whole animals. From 10 observations, we have found that the dry weight of the molt is on the average 13 % of the dry weight of the animal that sheds the molt. Assuming that the ash content of the molt is the same as the ash content of the integument of the whole animal, we estimate that 47 % of the body ash resides in the integument.

Ash content of brood pouch young was estimated from a large number of specimens taken from live females. A dry sample of 0.6 mg of newly hatched larvae had an ash content of 6.1 %. A sample of 1.2 mg of late stage larvae had an ash content of 6.6 %. Ash content of eggs was not determined; we assume that the ash content is slightly less than that of the newly hatched larvae, and we have used a value of 6.0 %.

Nitrogen and Carbon

Nitrogen content was determined by the micro-Kjeldahl method from three samples of mixed juvenile-adult animals. The dry weights of the samples were 12, 24, and 63 mg, and contained 13.1 %, 11.7%, and 11.2 % nitrogen respectively; the mean was 11.5 % of total dry weight. From a large number of determinations, Raymont et al. (1964) found a value of 11.4 % for *Neomysis integer*. Omori (1969) reported 11.0 % for *Siriella aequiremis,* and Jawed (1969) found 11.9 % for *Neomysis rayii.*

Carbon content was determined with an F and M carbon analyser model 180, described by Lasker (1966). We assume that all organic carbon, including that in chitin, is liberated by this method.

Three samples of females, without young, that weighed 0.2 to 0.4 mg, had carbon fractions between 35.6 % and 38.1 % of dry weight; the mean was 36.8 %. This estimate is intermediate among other values reported for mysids: *Lophogaster* sp. (family Lophogastridae) — 46.8 % (Curl, 1962a); *Neomysis integer* — 30.2 % and 29.5 % (Raymont et al., 1964, 1966); mixed mysids and euphausids — 40.7 % (Beers, 1966); *Siriella aequiremis* — 42.4 (Omori, 1969). From his analysis of several kinds of arthropods, Curl (1962a) found an average of about 38 % of the dry weight as carbon. He points out that this is about ¾ of the commonly assumed value of 50 % (Krogh, 1934).

In our carbon analysis of molts and young, we found that a 0.2-mg sample of fresh dried molts had 23.5 % carbon, a 0.4-mg sample of eggs had 58.0 % carbon, a 0.4-gm sample of midstage larvae had 47.1 % carbon. The carbon contents of the ash-free organic fractions of the material were calculated from these values. Lasker (1966) found 17 % carbon in the molts of *Euphausia pacifica* and 50 % carbon in the eggs.

Macromolecular Components

We assume that the body nitrogen of our species, *Metamysidopsis,* is present as protein, free amino acids, and chitin (Raymont, Austin, and Linford, 1968). We made no evaluation of chitin content, but used the value of 7 % determined for *Neomysis integer* by Raymont et al. (1964). The percent "protein" (may include free amino acids) was estimated by the following relationship, given that 16 % of "protein" is nitrogen, 6.5% of chitin is nitrogen, and 7 % of the dry body is chitin: 0.16 ("protein") + (0.065) (0.07) = 0.115. From this relationship, the "protein" content of the whole dry body was estimated to be 69 %, which is similar to the value to 71 % protein estimated directly by Raymont et al. (1964) for *Neomysis integer*. According to the estimates of Raymont et al. (1968), the percent nitrogen in proteins of Mysidae may be lower than the value of 16 % commonly assumed for animal tissues. They found 13.3% N in the body protein of *Neomysis integer*, and estimated that about 17 % of what we would have designated as "protein" nitrogen was actually free amino acid nitrogen. They suggest that the amino acids may function in osmoregulation for *Neomysis integer*, which is a euryhaline-brackish water species. We know nothing directly about this for *Metamysidopsis*. Our species lives in a constant oceanic salinity, and we estimated the ash content to be higher than that of *N. integer*. Therefore, a high concentration of free amino acids may not be necessary for osmoregulation in our species. Whatever the ratio of protein/free amino acids may be in *Metamysidopsis*, our energy calculations should not be affected materially.

The lipid content of the mysid bodies was estimated by placing samples of dried, crushed bodies successively for 1 hr in each of two 10-ml portions of ethyl alcohol and two 10-ml washes of petroleum ether. The lipid content was estimated as the difference in dry weight before and after extraction. Two dry samples of mixed animals, weighing 62.9 mg and 13.4 mg, gave values of 9 % and 11 % lipid respectively. A third sample, containing 24.1 mg of brooding females that had full complements of young in their brood pouches, gave a value of 19 % lipid. Linford (1965) found that large females of *Neomysis integer* carrying young had higher lipid contents than males. From our knowledge of the number of young per female and the estimated percent lipid in the young, we calculate that ¼ to ½ of the 19 % lipid value could be contributed by the brood pouch young. Therefore, we have excluded the 19 % value from our estimate, and we have used 10 % as the estimate of average lipid content of the dry bodies. This is slightly less than the value of 13 % estimated for *Neomysis integer* by Raymont et al. (1964), but within the range of means for three species estimated from a large number of determinations by Linford (1965): *Mesopodopsis slavveri* — 9.0 %; *Neomysis integer* — 10.1 %; *Praunus neglectus* — 9.3 %.

The carbohydrate content of the mysids was estimated as the amount of macromolecular material remaining after the average estimates for ash, protein, chitin, and fat are subtracted from the dry weight. This remainder is 1.5 %. Apparently the carbohydrate fraction is low in all pelagic Crustacea. Raymont and Conover (1961) found that 1 % of the dry weight of *Neomysis americana* was glucose; Raymont and Krishnaswamy (1960) found 1.3 % carbohydrate in dry *Neomysis integer;* and Raymont et al. (1964) found 2.4 % carbohydrate in dry *Neomysis integer*.

We did no detailed analyses of the composition of molts, but we assume that the molt is composed of structural materials rather than energy storage materials. Since we consider that carbohydrates and lipids are virtually absent, we entered zero values for them in Table 3. The "protein"/chitin relationship was determined indirectly. First, we estimated the amount of carbon in the average protein of the mysids from the relationship:

$$\begin{aligned}(\%\ \text{C as protein}) = {} & (\%\ \text{C in body}) \\ & - (\%\ \text{C as chitin}) \\ & - (\%\ \text{C as lipid}) \\ & - (\%\ \text{C as carbohydrate}).\end{aligned}$$

The percent carbon in the organic fraction of the body is 42 %, the chitin fraction is taken as 8 %, the chitin is assumed to be 50 % carbon (Curl, 1962a), the lipid content of the organic fraction is 11 %, the lipid is assumed to be 77 % carbon (Lasker and Theilacker, 1962), the carbohydrate fraction is about 2 %, and the carbohydrate is assumed to be 40 % carbon (Curl, 1062a). Therefore, the percent carbon in the mysid protein is calculated as:

$$\begin{aligned}\%\ C &= \frac{1}{0.79}[0.42 - (0.08)(0.50) - (0.11)(0.77) \\ &\quad - (0.02)(0.40)] \\ &= 0.364 \\ &= 36.4\ \%\end{aligned}$$

This is considerably less than the average value of 52 % carbon in protein given by Hawk, Oser, and Summerson (1954), but similar to an estimate of 37 % made from the data of Lasker (1966), and higher than an estimate of 23 % made from the data of Raymont et al. (1964).

The second step in finding the relationship between chitin and protein in the molts was to estimate the chitin fraction from the following relationship:

$$\begin{aligned}&(\text{chitin fraction})(\%\ \text{C in chitin}) \\ &\quad + (\text{protein fraction})(\%\ \text{C in protein}) \\ &= (\%\ \text{C in molt})\end{aligned}$$

where

$$\text{chitin fraction} + \text{protein fraction} = 1.0.$$

The chitin fraction calculated from this relationship is 44 % for the organic molt. The protein fraction is therefore estimated to be 56 %. This result suggests that a large fraction of the chitin may be reabsorbed by the animals before molting. This seems reasonable because in Crustacea the new endocuticle is formed during the intermolt period (between 2 % and 46 % of the time between molts, according to Passano, 1960).

To estimate the protein content of eggs and larvae, we have made some arbitrary assumptions that seem reasonable, and that do not measurably affect our energy calculations in any event. We have assumed that the eggs do not contain a measurable amount of carbohydrate, and that they contain little or no chitin because the integument is not yet formed. Therefore, we have assumed that the organic fraction of the eggs is either protein or lipid. For late stage larvae we have also assumed that carbohydrate is absent, but that some chitin is present because they form integument and molt once before they are released. We have assumed that the organic fraction of the larvae contains half the amount of chitin as the adults, or 4 %.

The protein-lipid composition of the eggs was calculated from the carbon content of the ash-free fraction. We have estimated (above) that 36.4 % of the mysid protein is composed of carbon, that 77 % of the lipid is carbon, and that 61.8 % of the ash-free egg is carbon. By using these values we calculate that the organic fraction of the eggs is 62.5 % lipid and 37.5 % protein. The carbon content of intermediate age brood pouch young (about 5 days old) was less than that of eggs and more than that of late stage larvae. For these intermediate age young we calculate a lipid content of 43 %.

ENERGY CONTENT

Juveniles - Adults

The ash-free calorie content of *Metamysidopsis* was determined in a Parr non-adiabatic calorimeter. The data, converted to ash-free values, are given in Table 4. Three of the samples contained so little material that Nujol supplement had to be added to raise the heat of combustion to a measurable level. All three of these measurements fell outside the 95 % confidence limits of the six determinations made without the Nujol supplement. The variability among the three supplemented determinations can be attributed to the ± 2 % variation of the caloric content of the Nujol supplement (10,791 ± 200 cal/g), because the weight of the supplement greatly exceeded the weight of the sample material in each case.

TABLE 4.—Ash-free[1] caloric content of *Metamysidopsis*.

Specimens	Dry weight	Calorie content
	Mg	*Cal/g*
Young juveniles	1.05	[2]3028.9
Juveniles	2.65	[2]6462.6
Young females	4.80	[2]4242.3
Advanced juveniles	12.55	5021.7
Immature males	17.30	5049.0
Immature males	17.30	5358.0
Mature males	15.75	5123.8
Mature females	12.40	5185.7
Mature females	17.25	5699.1

[1] Ash content 12.5 % used in all calculations.
[2] Nujol supplement used in determinations.

The mean for the six nonsupplemented samples is 5,240 cal/g (shown as 5.24 cal/mg in Table 3). No significant differences in energy content among developmental stages nor between sexes were found.

This mean calorie content estimate is somewhat lower than those reported for other crustacea. Slobodkin and Richman (1961) gave values of 5.4 to 5.6 cal/ash-free mg; Lasker (1965) reported a range of 4.9 to 5.4 cal/mg (including ash) for two species of copepods. Our mean value is also lower than the value that can be calculated from the information on body composition, together with reported average values of the calorie content of animal protein, fat, and carbohydrate. Conversion factors given by Morowitz (1968) are: protein, 5.5 cal/mg; fat, 9.3 cal/mg; and carbohydrate, 4.1 cal/mg. Since chitin is glucosamine, we have assumed that it, like carbohydrate, has a calorie content of 4.1 cal/mg. From these conversion factors and the composition data given in Table 3, we calculated an expected value of about 5.77 cal/ash-free mg.

We use the empirical value, 5.24 cal/ash-free mg, in our subsequent energy budget calculations. We consider this to be a conservative estimate, because it assumes that the mysid protein has an energy content of only 4.8 cal/mg. This lower than expected estimate may be related to the empirical observation that the mysid protein contains only 36 % carbon, rather than about 50 % as is commonly assumed for animal protein.

The juvenile and adult *Metamysidopsis* contained 12.5 % ash; therefore, the energy in the whole dry body of an adult or juvenile is estimated to be: (4.6 cal/mg) × (dry weight, mg).

Molts

We estimated the energy content of molts indirectly, because it was difficult to obtain enough material for calorie measurements. The ash-free fraction (55 %) of the molts was estimated to be composed of 44 % chitin and 56 % protein. By assuming that chitin has an energy content of 4.1 cal/mg, and that the mysid protein has an energy content of 4.8 cal/mg, we calculate that the ash-free fraction of the molts has an energy content of 4.5 cal/mg.

From a sample of 10 animals and their molts we found that the dry weight of molts is on the average 13 % (range 9-19%) of the dry weight of the animals that shed them. Lasker (1964, 1966) and Jerde and Lasker (1966) found that the dry molts of a euphausiid were about 10 % of the dry weight of the animals that produced them (range 4-14 %).

The energy lost by molting *Metamysidopsis* is therefore proportional to the size of the animal:

$$(0.13)\,(0.55)\,(4.5\ \text{cal/mg}) \times (\text{dry weight of animal, mg})$$

or

$$(0.32\ \text{cal/mg}) \times (\text{dry weight of animal, mg}).$$

Eggs and Larvae

We estimated that eggs were 6 % ash, 35 % protein, and 59 % lipid. The energy content of an egg is estimated to be: (0.35) (4.8 cal/mg) + (0.59) (9.3 cal/mg) = 7.16 cal/mg. A sample of 140 eggs was dried and weighed; the mean dry weight per egg was 0.0055 mg. The energy content per egg is therefore 0.039 calorie.

We estimated that, just before being released from the brood pouch, the larvae are about 6 % ash, 61 % protein, 29 % lipid, and 4 % chitin. The energy content of a late stage larva is estimated to be: (0.61) (4.8 cal/mg) + (0.29) (9.3 cal/mg) + (0.04) (4.1 cal/mg) = 5.78 cal/mg. The mean dry weight per larva, estimated from 110 individuals, was 0.0051 mg. The energy content per larva is therefore 0.029 calorie.

ENERGY BUDGET AND EFFICIENCY OF ENERGY TRANSFER

From the data on average growth, age-specific fecundity, respiration rate, and energy content we have calculated cumulative curves of energy use by individual mysids in attaining various stages of development. Data on age-specific natural mortality rates (Fager and Clutter 1968) were used to estimate l_x (probability of animal being alive at age x) schedules and average generation time of the field population. The field and laboratory data were combined in an analysis of the efficiency of energy transfer through the *Metamysidopsis* population to the organisms that feed on them.

CUMULATIVE ENERGY CURVES

At age zero the egg contains about 0.04 cal. Ten days later, at the time it is released from the brood pouch, the larva contains about 0.03 cal. Thereafter the average calorie content increases in proportion to the dry weight (4.6 cal/mg). The average schedules of energy incorporation differ between males and females after about 30 days; the rate of incorporation becomes lower and levels off sooner in males. The accumulation of body energy is shown as the lowest curves in Figure 12 (females) and Figure 13 (males).

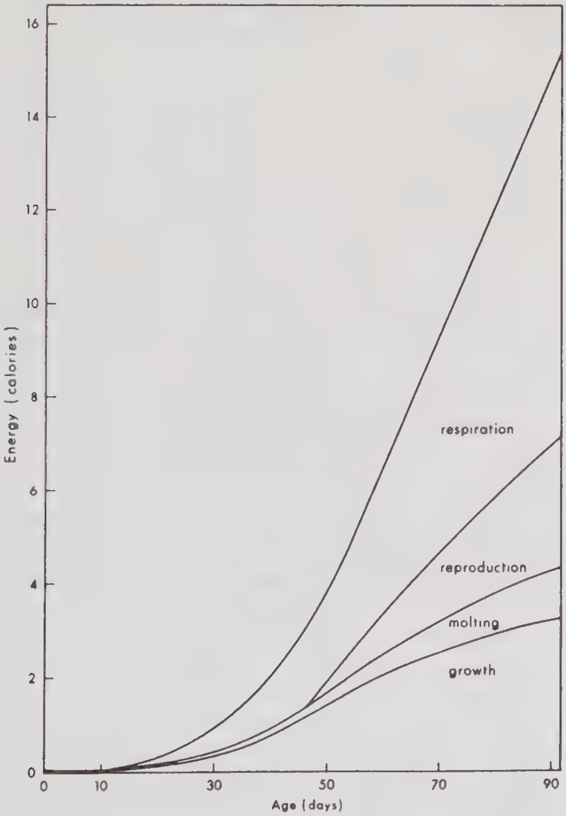

FIGURE 12.—Cumulative energy used by individual *Metamysidopsis* females. The curves are additive, i.e. the space between the lower two curves represents the cumulative energy lost in molts, the next higher space represents energy used to produce eggs (both fertilized and unfertilized), etc.—so that the upper curve represents cumulative energy used for all processes.

The amount of energy lost in molts varies with age because the size of the molt increases and the molting frequency decreases. Females and males have different cumulative losses of energy from molting because their growth rates are different after age 30 days, and their molting frequencies are different (Table 1.) Although the actual loss of energy in molting occurs at discrete intervals, we have plotted the cumulative energy loss as smooth curves, because the accumulation of energy for integument formation probably is continuous. Cumulative energy loss in molting is shown as the second curve in Figure 12 (females) and Figure 13 (males). The cumulative energy curves are additive, i.e. the area between the first curve (body energy) and second curve (molting energy) represents the cumulative energy loss in molts.

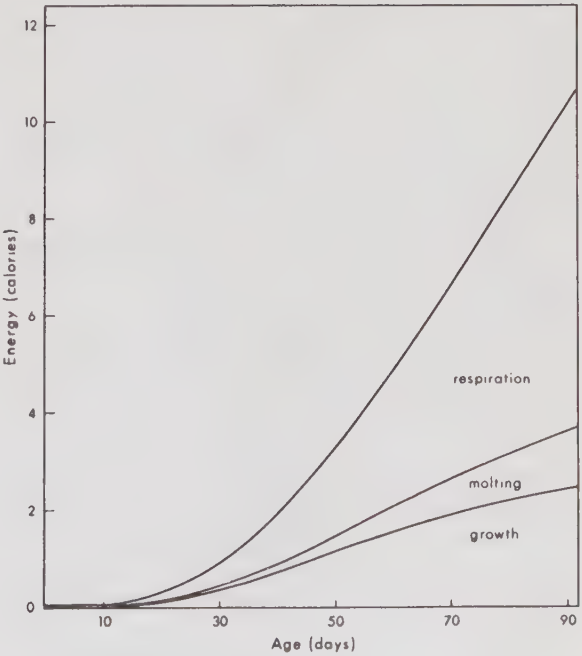

FIGURE 13.—Cumulative energy used by individual *Metamysidopsis* males. The curves are additive (see Fig. 12).

Males use a small amount of energy in producing sperm, but we assume that this is negligible. In females, the ova begin to be infused with yolk about age 45 days. The actual discharge of eggs occurs at discrete intervals of about 10 days, beginning at age 53 days. We assume that the accumulation of energy for reproduction is more continuous than this, therefore we have shown reproductive energy use as a smooth curve. The reproduction energy curve shown in Figure 12 is based on the maximum fecundity estimate given previously [number of eggs = 4.1 (body length, mm) — 8.9]. A reproduction energy curve based on our minimum estimate of fecundity [number of eggs = 4.1 (body length, mm) — 12.0] would be 0.12 cal (3.1 eggs) lower per spawning. This would make the minimum estimate 72 % of the maximum estimate at the age of first spawning (53 days) and progressively higher in percentage thereafter, e.g. 85 % at the age of fifth spawning (93 days). All our reproduction energy calculations take into account the observation that, on the average, mature females extrude the usual number of eggs only one-half of the time and otherwise extrude only one-half the usual number of eggs.

The amount of energy used in respiration was calculated from the weight-specific respiration equation: $R' = 2.1$ (dry weight, mg)$^{-0.33}$, and from energy conversion factors based on our estimates of body composition.

We do not know what substrate *Metamysidopsis* catabolizes. The organic fraction of the body is largely protein; the storage product (carbohydrate and lipid) content is low. Raymont and Krishnaswamy (1960) observed that the carbohydrate content of *Neomysis integer* decreased slightly, from about 1.30 % (of dry weight) to 1.06 %, when a marked reduction in feeding occurred. For the same species, Linford (1965) found no significant change in lipid level whether the animals were starved, fed a lipid-free diet, or fed a high lipid diet. Raymont et al. (1968) asserted that *N. integer* uses protein as an energy source.

We agree with Linford (1965) that it seems likely that the mysids must live largely on their daily ingestion. We think that the food they ingest has composition similar to their bodies. Therefore, our energy calculations assume that they use catabolic substrates in proportion to their presence in the body. This is supported by the results of Jawed (1969). To convert the amount of oxygen used in respiration into the equivalent energy lost as heat we have used the following values for calories lost/μl O_2 consumed (Hawk et al., 1954; Prosser, 1950): protein, 4.5×10^{-3}; lipid, 4.7×10^{-3}; carbohydrate, 5.0×10^{-3}. Therefore, our estimate of the average amount of energy used in respiration is about 4.5×10^{-3}cal μl O_2.

The cumulative energy used in respiration is shown as the uppermost curve in Figure 12 (females) and Figure 13 (males). The area between that curve and the next lower curve represents the catabolic heat loss. These respiration data were calculated for a temperature of 16° C, which was the median temperature of the natural environment of *Metamysidopsis.* Our respiration measurements were made in flowing water during the daylight hours. Therefore, they represent basal metabolism + energy expended in active swimming. There is some evidence (Clutter, 1969) that the mysids may be less active at night, even though they continue to swim at all times. For this reason we think that the field population may use somewhat less than this amount of energy in respiration.

Our estimated rate of energy loss in catabolism is higher than that estimated by Jawed (1969) in his study of nitrogen excretion in *Neomysis rayii.* He suggested that protein is catabolized in relatively large quantities, therefore nitrogenous excretion may provide a good estimate of catabolism. He found an average catabolism of about 2.5 % of body nitrogen per day in adult animals that were probably 8 to 10 mg dry weight, that were held at 10° C. The rate for adult *Metamysidopsis* of average size (0.6-0.8 mg) was 5 to 6 % of the body energy per day. This disparity in catabolism may result from differences between the size and between the environmental temperatures of the two species.

Jawed (1969) showed that about 15 % of the nitrogen was excreted as amino acids. We did not investigate this in *Metamysidopsis*, therefore, our estimate of total catabolism could be slightly low because it includes only losses of heat energy.

NET ECOLOGICAL EFFICIENCY

Mortality and Generation Time

Estimates of natural mortality in the field population were made during the same period that the laboratory growth experiments were done (Fager and Clutter, 1968).

Brood pouch mortality rate was estimated to be 0.013/day (maximum of 0.017/day). Mortality rates for juveniles, immatures, and adults were estimated from consecutive series of field collections. The field mortality rates varied during the year. Survival curves (l_x = probability of being alive at age x) for periods of at least mortality, median mortality, and greatest mortality are shown in Figure 14. The mortality rates that we used to calculate these l_x curves are shown in Table 5. The greatest mortality rate results in a declining population; at the median mortality rate the population size remains about constant; and at the least mortality rate the population increases.

An average female first reproduces at about age 53 days. The generation length for the population is somewhat longer because the females reproduce more than once. The generation length for the field population varied between 67 days and 71 days; the median was 68 days (Fager and Clutter, 1968).

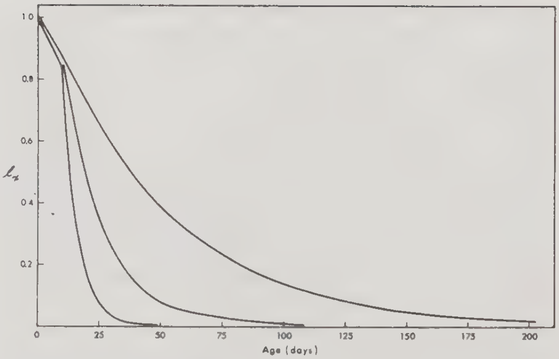

FIGURE 14.—Age specific survival (l_x = probability of being alive at age x) of *Metamysidopsis* calculated from estimates of greatest, median, and least mortality in the field population (Table 5).

TABLE 5.—Mortality rates (per day) used to calculate l_x schedules for the *Metamysidopsis* field population.

Specimens	Least mortality	Median mortality	Greatest mortality
Brood pouch young	0.013	0.013	0.017
Juveniles	0.02	0.06	0.15
Immatures	0.02	0.05	0.14
Adults	0.02	0.04	0.13

Relative Energy Use by Individuals

We determined the calories of energy used by average individual female and male mysids, and the fractions used for growth, molting, reproduction, and respiration from the estimates of cumulative energy use (shown in part in Figures 12 and 13). The amounts and the percentage distributions required to reach selected stages of development are shown in Table 6.

TABLE 6.—Energy used by individual *Metamysidopsis* to reach selected stages of development.

			Relative use			
	Age	Energy	Respiration	Reproduction	Molting	Growth
	Days	*Cal*	*%*	*%*	*%*	*%*
Females:						
Egg yolk production	45	2.7	52	0	8	40
First reproduction	53	4.6	49	9	7	35
Generation	68	8.7	50	15	7	28
l_x = 0.01	[1]103	18.4	55	19	7	19
Males:						
Maturity	48	3.0	54	0	10	36
l_x = 0.01	[1]103	12.8	67	0	12	21

[1] Approximate age at which l_x = 0.01 in a nearly stable population ($r \sim 0$).

The indicated age at which the probability of being alive reaches 0.01 applies to the stable population (median death rates).

The males require less energy to reach maturity than females, but relatively more of this energy goes into molting and respiration and less is incorporated. Two-thirds of the energy used in reproduction remains in the population; one-third is lost as unfertilized eggs.

The estimates of relative use of assimilated food by *Metamysidopsis* females during a life span are compared with estimates for a copepod and a euphausid (Corner, Cowey, and Marshall, 1967) in Table 7. The mysids apparently use a fraction of assimiliated energy for growth that is intermediate between the other two species, a lower fraction for metabolism, and a higher fraction for producing eggs.

TABLE 7.—Use of assimilated food by *Metamysidopsis* females (life span 103 days) compared with the copepod *Calanus finmarchicus*[1] (life span 10 weeks) and the euphausid *Euphausia pacifica*[2] (life span 20 months).

	Assimilated energy used by *Metamysidopsis*	Assimilated N used by *Calanus*	Assimilated C used by *Euphausia*
	%	%	%
Growth	19	25.3	10.1
Metabolism	55	61.4	72.3
Molts	7	0.9	16.6
Eggs	19	12.4	1.0

[1] From Corner, Cowey, and Marshall (1967).
[2] From Lasker (1966), revised in Corner et al.

Relative Energy Use by the Population

The values of relative energy use given in Tables 6 and 7 apply to individuals, or to populations wherein all members live a full life span. They do not apply to the natural population, because some die during all stages of growth.

We have estimated the relative amounts of energy that would be lost by populations in respiration, production of infertile eggs, molting, and mortality at the observed minimum, median and maximum mortality rates shown in Table 5. This was done by calculating the fraction of the population that died during each intermolt period ($\triangle l_x$), and multiplying this times: (1) the mean body energy content for the midpoint of that period, (2) the quantity of cumulative energy lost in infertile eggs up to the midpoint of that period, and (4) the quantity of cumulative energy used in respiration up to the midpoint of that period. The product values for each of these loss categories (mortality, molting, etc.) were then summed over all ages (to $l_x \sim 0.001$). The relative energy use values were calculated as fractions of the overall sum for all categories combined. We excluded fertilized eggs because this reproduction energy is retained in the population.

The age specific distribution of energy use (representing energy loss, because fertilized eggs are excluded) by a population (females and males) of *Metamysidopsis* at the median mortality rate is illustrated in Figure 15. All the curves are plotted with reference to the base line, zero. The rate of energy loss is low among eggs and larvae, and much higher among the juveniles that have just emerged from the brood pouch and begun to swim. In the larger animals, the respiration per unit weight is lower, but the respiration per animal is higher, so that the respiration rate per day is highest among the animals that are about 25 days old. The loss of energy per day from all causes is highest among the animals that are about 30 days old. After this the curve declines because the effect of larger size becomes less than the effect of smaller numbers.

The estimated relative amounts of energy lost by the population of females, males, and both sexes combined, for each loss category and

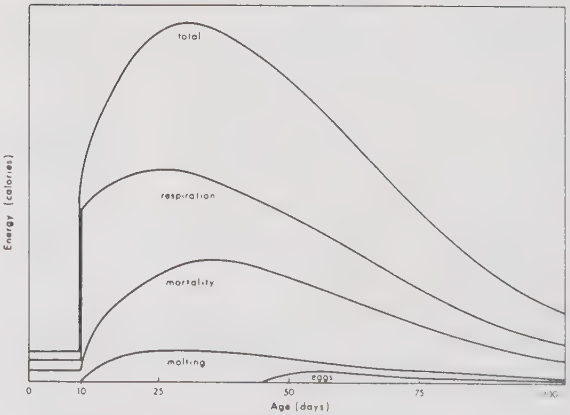

FIGURE 15.—Age specific distribution of energy loss by a *Metamysidopsis* population at the median mortality rate. Production of fertilized eggs is excluded.

for each of three mortality rates, are shown in Table 8. The percentages for females and males combined are not quite the same as the means of the separate percentages for females and for males. At the minimum death rate 55 % of the energy loss would pass through the female half of the population (58 % if fertile eggs are included). At the median death rate 52 % would pass through the females, and at the maximum death rate, 50 %.

TABLE 8.—Relative amount (%) of energy lost by *Metamysidopsis* populations in respiration, production of infertile eggs, molting, and mortality; at minimum, median and maximum mortality rates.

Sex	Death rate	Respiration	Infertile eggs	Molting	Mortality
		%	%	%	%
Females	minimum	63.7	6.7	8.6	20.9
	median	55.6	3.7	7.7	33.0
	maximum	45.4	0.1	6.1	48.4
Males	minimum	67.4	0.0	12.6	20.0
	median	58.3	0.0	9.9	31.8
	maximum	47.9	0.0	6.5	45.6
Females and Males	minimum	64.5	3.7	10.4	20.5
	median	56.9	1.9	8.8	32.4
	maximum	46.7	0.1	6.3	47.0

If we assume that all the mortality is yield to predators (Odum and Smalley, 1959; Engelmann, 1961), our mortality fractions are an estimate of net ecological efficiency (energy yield/energy assimilated). Apparently some Crustacea regularly die from natural causes other than mortality (e.g. *Daphnia,* Slobodkin, 1959). Many mysids of all ages died in our laboratory cultures, but we do not attribute this to senescence. In the field and in the laboratory we observed *Metamysidopsis* much older than the oldest animals that are involved significantly in our energy calculations. Our best estimate of the net ecological efficiency of the mysid population, for transfer of energy to a higher trophic level, such as fishes, is about 32 %. The net efficiency of transfer to all trophic levels is 1 — respiration fraction = 43 %.

ASSIMILATION AND GROSS ECOLOGICAL EFFICIENCY

Assimilation Efficiency

Gross ecological efficiency (energy yield/energy ingested) is the product of net ecological efficiency (energy yield/energy assimilated) × assimilation efficiency (energy assimilated/energy ingested). Therefore, an estimate of assimilation efficiency is required to estimate gross ecological efficiency for the mysid population.

We attempted to estimate the assimilation efficiency of *Metamysidopsis* directly by a carbon-14 method described by Lasker (1960). This failed because the mysids did not filter sufficient amounts of radioactive phytoplankton. An experiment with another member of the family Mysidae, taken from the same area, was successful. This gave an estimate of 90 % assimilation efficiency.

Lasker (1966) obtained a similar high value (84 %) for the morphologically similar *Euphausia pacifica;* and Marshall and Orr (1955) found values greater than 90 % for the copepod *Calanus finmarchicus.* In his detailed reviews of assimilation in zooplankton, Conover (1964, 1966) suggests that these values probably are too high. The very large number of observations, many of them his own, that are cited by Conover seem to be evidence that, although variable, the mean assimilation efficiency for crustacean zooplankton is at least 60 % and perhaps greater.

Gross Ecological Efficiency

From the information presently available we consider that the assimilation efficiency of the mysids is between 60 % and 90 %. Our best estimate of net ecological efficiency (yield/assimilated) is 32 %. Therefore, the minimum estimate of gross ecological efficiency (yield/ingested) is 19 % and the maximum estimate is 29 %.

These estimates are well within the broad range of available estimates of gross ecological efficiency (see reviews by Patten, 1959; Slobodkin, 1961; Phillipson, 1966; Reeve, 1966), and within the range of 8 % to 30 % that Engelmann (1961) considers to be acceptable. They are about 2 to 3 times as high as the median value of 10 % that is suggested by Slobodkin (1961, 1962), but lower than the values of 30 % to 50 % suggested for marine zooplankton by

Ketchum (1962), Steemann Nielsen (1962), and Curl (1962b).

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CHARACTERISTICS OF SEA-SURFACE TEMPERATURE ANOMALIES

L. E. Eber[1]

ABSTRACT

Sea-surface temperature anomalies in the North Pacific Ocean, constructed from a 14-year series (1949-62) of monthly mean charts, exhibit numerous instances of quasi-stationary behavior. Selected examples from this series reveal a recurring pattern in which the principal feature is a positive or negative cell in the anomaly field, located approximately between lat 30° N and 50° N. The cell in this pattern is partially encircled by anomalies of opposite sign to the north, east, and south in a zone contiguous with the North American coast. This anomaly configuration, viewed with consideration of the associated sea-temperature field, suggests the existence of a standing wave in the current structure. Such a wave could affect the partitioning of the West Wind Drift Current as it approaches the coast and splits into northward and southward flowing branches. Physical data for verification of a standing wave are not available, but dimensional attributes inferred from the sea-temperature anomaly structure conform loosely to theoretical constraints.

The temperatures in the upper mixed layer of the ocean undergo annual cycles, induced by seasonal heating and cooling, which vary from year to year. This variation can be expressed in terms of departures from the mean annual temperature cycle obtained by averaging over a number of years. The magnitudes, areal distributions, and time changes of such departures define anomalous conditions in the surface layer of the sea.

The 14-year series, 1949-62, of monthly sea-surface temperature charts, published by Eber, Saur, and Sette (1968), provides a base for studying temperature variations in the North Pacific Ocean. Monthly anomaly charts were constructed from this series by taking the difference between the sea-surface temperature fields for each month and year and the corresponding monthly normal fields. The latter were obtained by computing the 14-year averages, by month, at grid points. A number of selected examples are presented here to show the character of some of the prominent and long-lasting anomalies that occurred in the North Pacific Ocean between 1949 and 1962.

Many of the features to be discussed are in the vicinity of the transition zone between the subarctic and subtropic oceanographic regions as described by Tully (1964). Through this zone, which is located approximately at lat 35° N to 45° N between long 160° E and 140° W, the surface current flows eastward as the West Wind Drift. The mean surface temperature distribution in this region is essentially zonal with isotherms oriented along the circles of latitude. The chart of the 14-year average for October (Figure 1) illustrates these characteristics. As the West Wind Drift approaches the North American coast, it splits. One part turns north and moves in a counterclockwise trajectory around the Alaska Gyre and the other part turns south to become the California

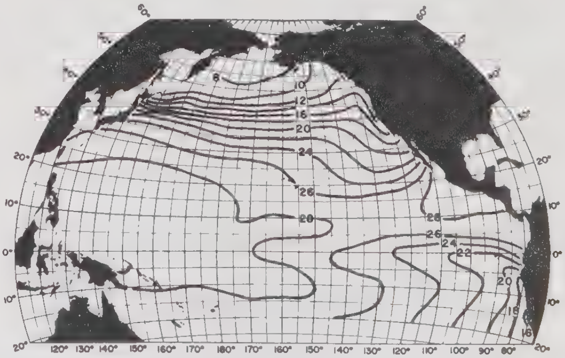

FIGURE 1.—Average sea-surface temperatures of the North Pacific Ocean in October, based on data from the 14-year period 1949-62.

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Current. The sea-surface isotherms, correspondingly, bend north and south, effecting a much-reduced temperature gradient parallel to the coast.

BEHAVIOR OF SEA-SURFACE TEMPERATURE ANOMALIES

To facilitate description, I shall designate as "warm" or "cold" cells, areas where the magnitude of departure from normal was 1° C or greater. The evolution of an anomaly can be readily followed by noting the configuration of its principal cell, or cells, in successive months. This is evident in the figures used to illustrate selected examples (Figures 2-30). These show the sizes and locations of the principal cells, enclosed by heavy lines representing a magnitude of 1° C, in the regions relevant to the discussion. The cells are marked by plus or minus symbols according to the sign of the anomalies. The thin lines represent the zero anomaly contour separating areas of below normal temperature (hatched areas) from those where the temperature was above normal.

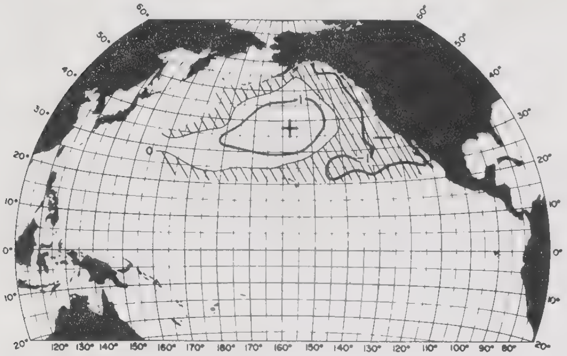

FIGURE 2.—Sea-surface temperature anomaly for January 1949. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

A good example of persistence was the warm anomaly present in the eastern North Pacific throughout most of 1949. In January the warm cell (defined by the 1° C anomaly contour) covered most of the area from lat 30° N to 45° N and long 145° W to 180° W. Maximum intensity of the positive departures from normal within this cell exceeded 3° C. Off the North American coast, the temperature anomalies were negative, with magnitudes greater than 1° C in a broad zone from Alaska to the tip of Baja California.

Figures 3-5 show subsequent positions of the warm cell in March, July, and October, respectively. The maximum intensities waxed and waned over this time period, dropping in March, increasing again to more than 3° C in July and diminishing once more in October. Except for a slight northward shift, the warm cell remained essentially stationary. During most of the period, negative anomalies prevailed in the coastal

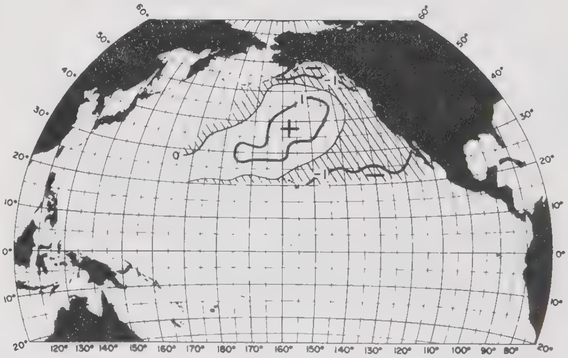

FIGURE 3.—Sea-surface temperature anomaly for March 1949. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

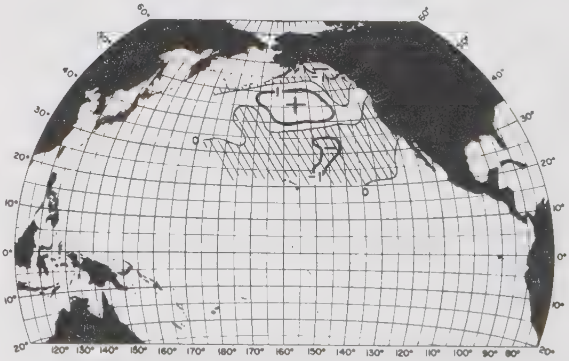

FIGURE 4.—Sea-surface temperature anomaly for July 1949. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

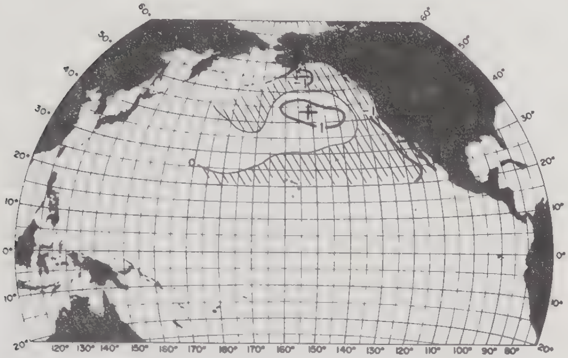

FIGURE 5.—Sea-surface temperature anomaly for October 1949. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

zone and in a southwestward tongue below 30° N but with fluctuating magnitudes.

The warm cell shrank in November and lost its specific identity in December. However, the general configuration of the colder than normal coastal zone and warmer than normal offshore region persisted through the winter and spring of 1950. In May 1950, the positive anomalies intensified and spread westward to Japan. The pattern stabilized in June and July marked by prominent warm cells in the east and far west portions of the positive area (Figure 6). At the same time, a cold cell in the Gulf of Alaska had begun to grow and push southward; this movement continued through September (Figure 7) accompanied by an eastward expansion of the warm belt. Ultimately, there was a deformation of the broad-scale pattern which had for many months dominated the central and eastern North Pacific, as negative anomalies spread through the Gulf of Alaska.

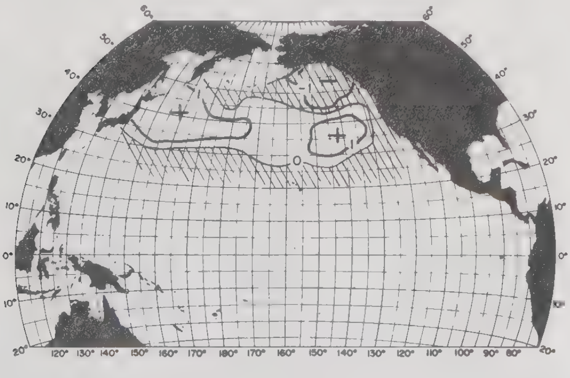

FIGURE 6.—Sea-surface temperature anomaly for July 1950. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

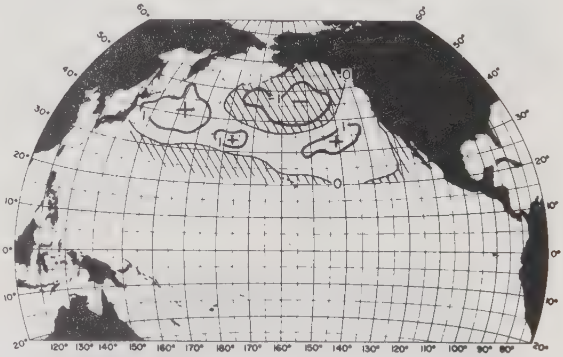

FIGURE 7.—Sea-surface temperature anomaly for September 1950. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

The years 1951-54 presented no striking examples of persistent sea temperature anomalies. Some relatively large-scale anomalies did develop in this period but they were short-lived. Much of the time the anomaly field was flat and featureless. Midway through 1955, however, a long-term progression of events began to evolve with the development of an anomaly pattern which was characterized by a positive belt that stretched eastward from Japan and a negative zone along most of the North American coast. The anomaly field intensified in August (Figure 8) when maxima exceeded 2° C in the warm cell and an extensive cold area was present in the coastal zone with negative departures exceeding 1° C in magnitude. The negative area stretched southwestward below lat 30° N. This pattern prevailed through November 1955 (Figure 9) but became weaker in December. In January 1956, the positive area contracted to the west while the region of negative anomalies to the east became flat and disorganized. Figure 10 shows the situation in February 1956. The

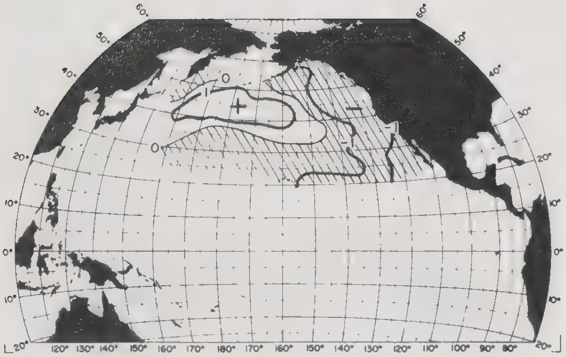
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FIGURE 8.—Sea-surface temperature anomaly for August 1955. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

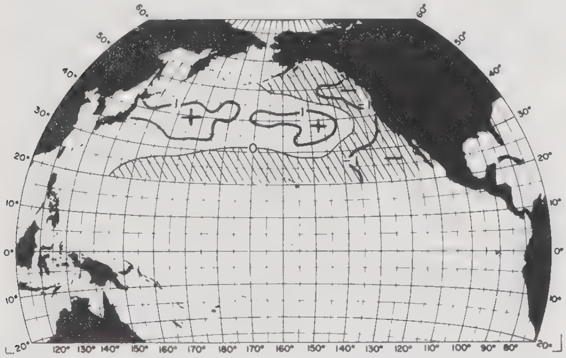
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FIGURE 9.—Sea-surface temperature anomaly for November 1955. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

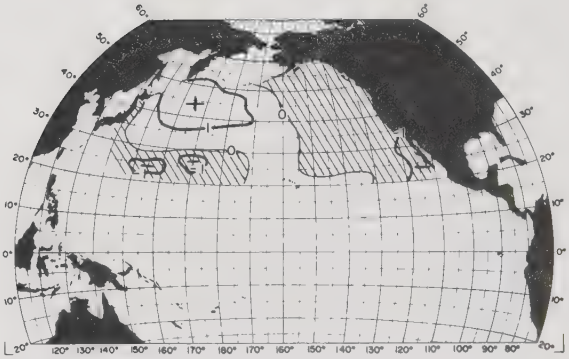
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FIGURE 10.—Sea-surface temperature anomaly for February 1956. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

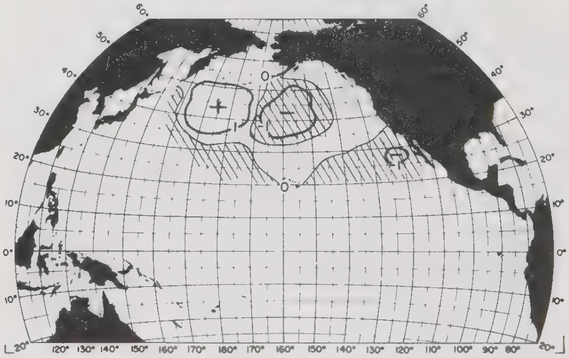
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FIGURE 11.—Sea-surface temperature anomaly for August 1956. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

warm cell at lat 36° N to 50° N, long 175° W to 150° E was the only prominent feature in evidence and remained so until August 1956, when a large cold cell developed just east of it (Figure 11). This latter feature was short-lived, however, and during the next few months the positive area once again expanded eastward while the tendency of anomalies along the North American coast changed from variable to predominantly negative. The chart for November 1956 (Figure 12) depicts the result of this process.

Transition to a second phase in the long-term evolution of the anomaly field was foreshadowed by a small cold cell at lat 25° N to 30° N, long 160° E to 170° E (Figure 12). This cold cell grew in size but remained in about the same location through March 1957 (Figure 13) while the area of positive anomalies edged toward the North American coast. The transition was complete by June, when the cold cell shifted north and stretched eastward in a belt of negative anomalies between lat 30° N and 40° N (Figure 14). Positive values prevailed in the Gulf of Alaska and along the North American coast, effecting an almost complete reversal from the late 1955 pattern.

The negative anomalies in the west central sector, long 175° W to 160° E, contracted to form

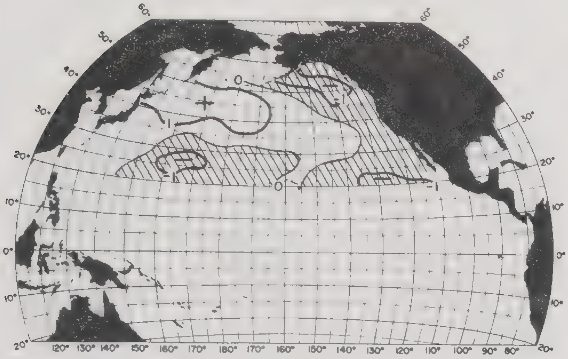
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FIGURE 12.—Sea-surface temperature anomaly for November 1956. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

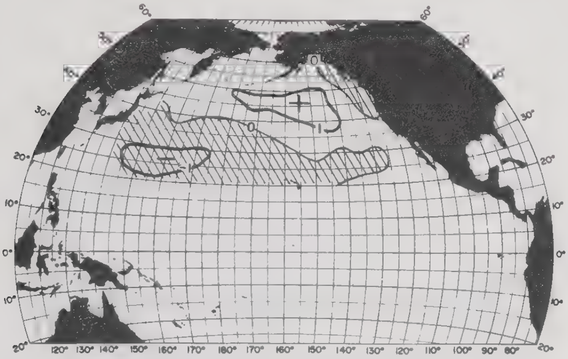
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FIGURE 13.—Sea-surface temperature anomaly for March 1957. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

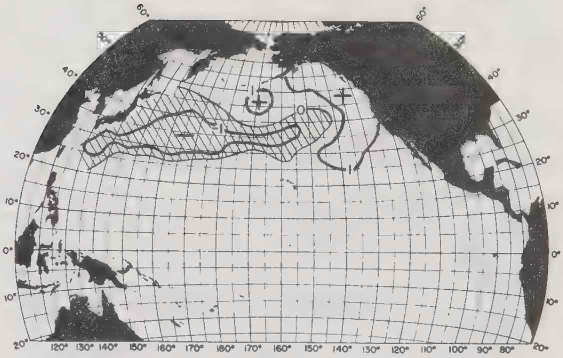
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FIGURE 14.—Sea-surface temperature anomaly for June 1957. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

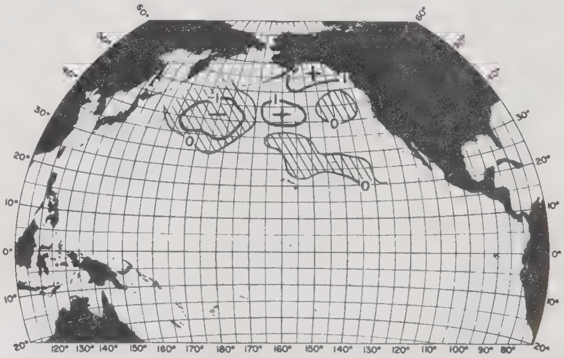
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FIGURE 15.—Sea-surface temperature anomaly for August 1957. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

a single prominent cell which, in August 1957, was centered at about lat 40° N, long 175° E (Figure 15). This feature remained fairly steady through November 1957 (Figure 16), but all remnants of the cold anomalies in the east sector vanished.

The cell structure in the negative anomaly deteriorated at the beginning of 1958, but reformed in March with the cold cell east of its earlier position, at lat 30° N to 40° N, long 145° W to 170° W (Figure 17). Further fluctuations took place in the negative region until August 1958, when a dominant cold cell appeared at lat 35° N to 50° N, long 150° W to 175° W (Figure 18). The zone of positive anomalies along the North American coast was strongly developed during most of 1958 and 1959. However, the emphasis in the distribution shifted to the south after mid-1958, and the warm tongue reaching southwestward, south of lat 30° N, was most intense in the early months of 1959 (Figures 19 and 20).

Elsewhere the pattern tended to be somewhat weak and disorganized, and remained so until November 1959, when prominent cells, in which departures from normal exceeded 2° C, were evident in the central oceanic region of negative anomalies and in the positive coastal zone

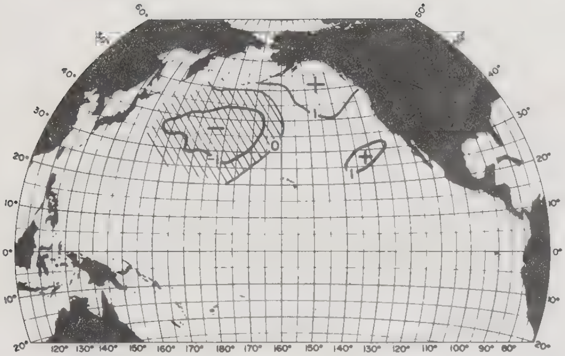
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FIGURE 16.—Sea-surface temperature anomaly for November 1957. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

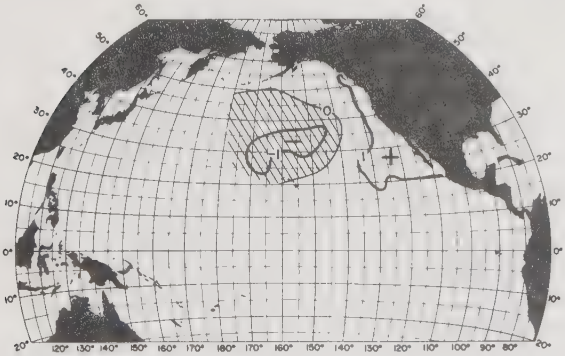
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FIGURE 17.—Sea-surface temperature anomaly for March 1958. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

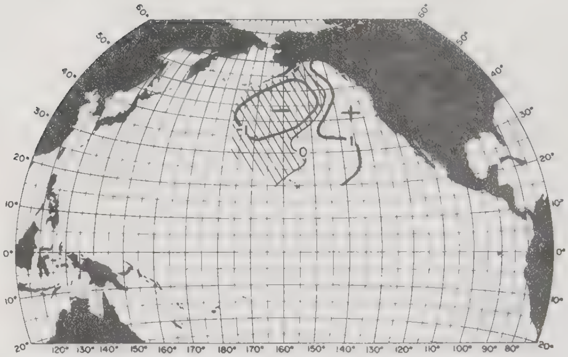
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FIGURE 18.—Sea-surface temperature anomaly for August 1958. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or (−) cells.

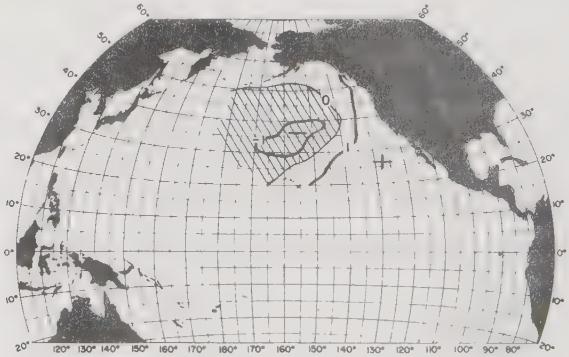
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FIGURE 19.—Sea-surface temperature anomaly for January 1959. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

(Figure 21). The intensity and size of the warm cells diminished by February 1960 (Figure 22) and anomalies along the North American coast were generally weak, although mostly positive, through mid-1961.

The cold cell present in the west central Pacific in November 1959 had, by February 1960, pushed eastward to a new location, at lat 32° N to 48° N, long 155° E to 155° W (Figure 22). Thereafter it remained essentially within this region until the spring of 1961. However, the size and shape of the cold cell fluctuated considerably during this extended interval, as indicated in the charts for June 1960, November 1960, and February 1961 (Figures 23-25). This cold cell began to shift eastward in May 1961 and, by June, had reached a position at lat 32° N to 45° N, long 137° W to 160° W (Figure 26) where it remained through August. A new warm cell had appeared in the west sector at lat 30° N to 40° N, long 170° W to 165° E in June, but cannot easily be related to an impending transition in the anomaly field. It appeared to shift westward in July and August then vanished in September 1961, when the overall pattern collapsed.

The third and final phase in the progression of events began rather abruptly in October 1961

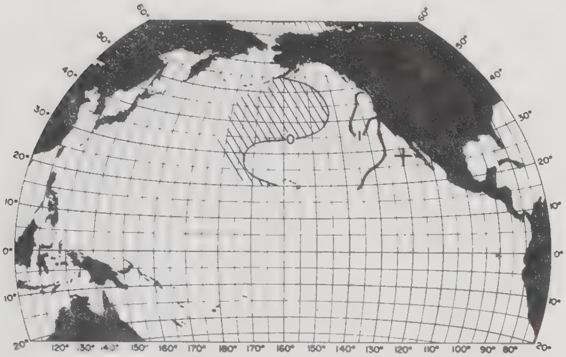
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FIGURE 20.—Sea-surface temperature anomaly for March 1959. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

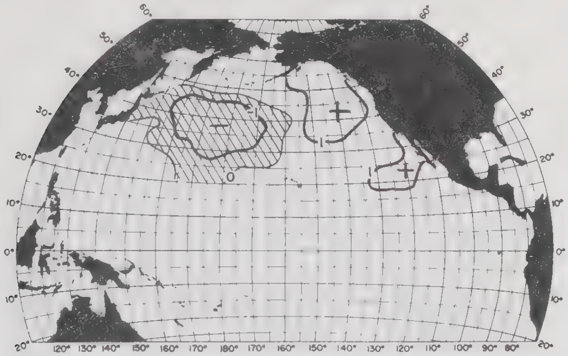
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FIGURE 21.—Sea-surface temperature anomaly for November 1959. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

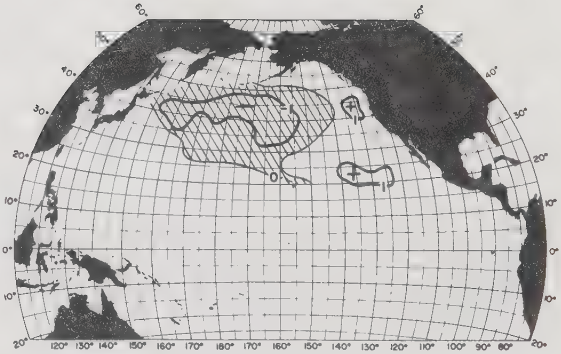
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FIGURE 22.—Sea-surface temperature anomaly for February 1960. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

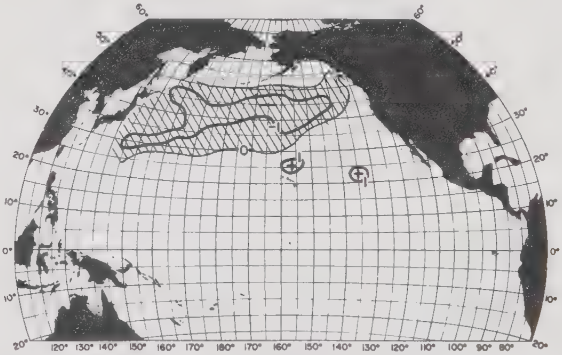
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FIGURE 23.—Sea-surface temperature anomaly for June 1960. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

with a second reversal of the anomaly field in the central and eastern North Pacific Ocean (Figure 27). The principal feature of the new pattern was a warm cell which developed at lat 35° N to 45° N, long 145° W to 175° W. Departures from normal temperatures along the coastal zone and in the region to the southeast of the warm cell were weak but predominantly negative. In a broad sense, this distribution remained essentially undisturbed for nearly a year. The warm cell shifted eastward in January 1962 (Figure 28), diminished in size and intensity in March and April, but revived in June 1962 (Figure 29). A second warm cell was present at that time, but did not retain a separate identity for long. The original warm cell began a westward movement which, by September (Figure 30), returned it to the same location it occupied 11 months earlier in October 1961 (Figure 27).

MAINTENANCE OF PERSISTENT ANOMALIES

The examples described in the preceding section depict a recurring pattern in the distribution of sea-surface temperature anomalies. Schematically, the principal features consist of

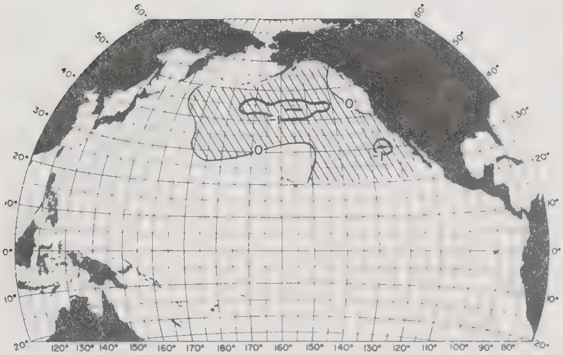
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FIGURE 24.—Sea-surface temperature anomaly for November 1960. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

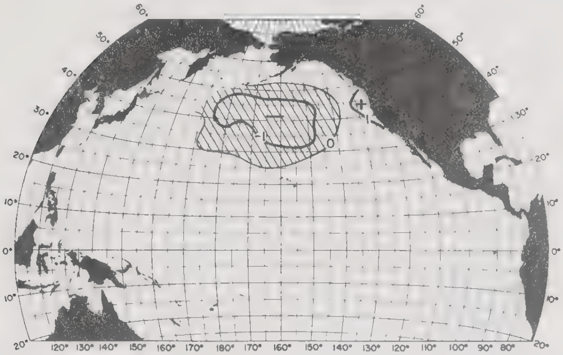
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FIGURE 25.—Sea-surface temperature anomaly for February 1961. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

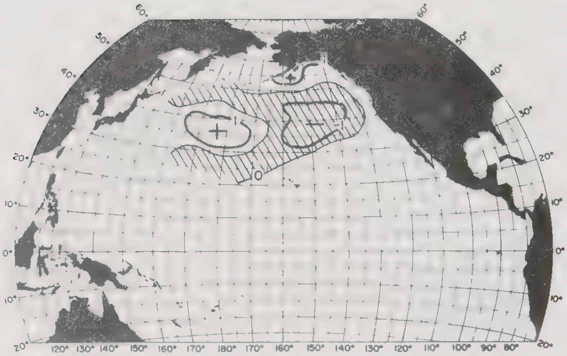
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FIGURE 26.—Sea-surface temperature anomaly for June 1961. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

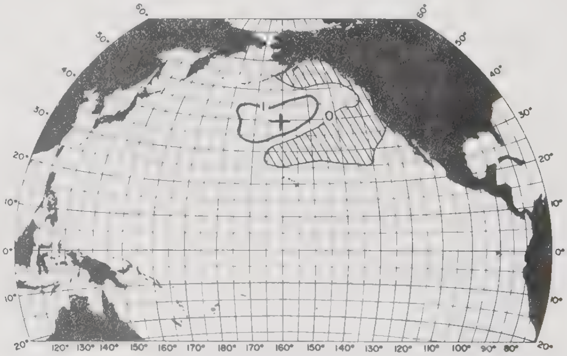
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FIGURE 27.—Sea-surface temperature anomaly for October 1961. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

a dominant, quasi-stationary cell in a latitudinal belt of either positive or negative anomalies, located approximately between lat 30° N and 50° N, partially encircled by anomalies of opposite sign to the north, east, and south, in a zone contiguous with the North American coast. The dominant cell in this model is embedded in the North Pacific West Wind Drift Current. It reflects a wavelike displacement of the isotherms, which normally are very nearly zonal from about long 150° E to 140° W in the vicinity of lat 40° N.

The fact that this cell, which defines an area of maximum departure from normal in the temperature field, is not propagated eastward with the ocean current suggests the existence of a standing wave, or perturbation, in the current structure. Assuming this to be so, water entering the wave would turn north (or south) of its normal course, cutting across the normal isotherms and thereby causing anomalous local advection of high (or low) temperature. Downstream from the point of maximum excursion the water cuts back toward its original course and temperature conditions revert toward normal. Because the temperature gradient across the West Wind Drift Current is moderately strong, a small displacement of the isotherms

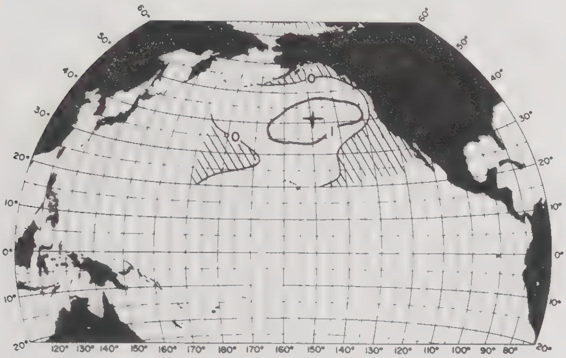

FIGURE 28.—Sea-surface temperature anomaly for January 1962. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

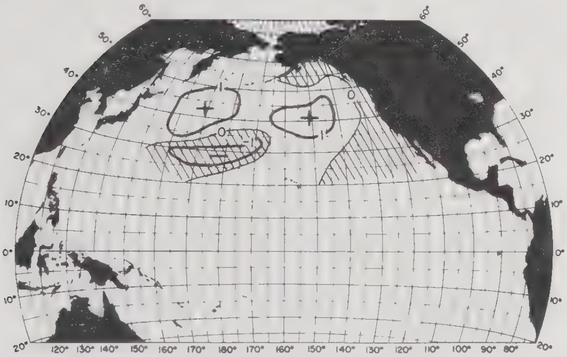

FIGURE 29.—Sea-surface temperature anomaly for June 1962. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

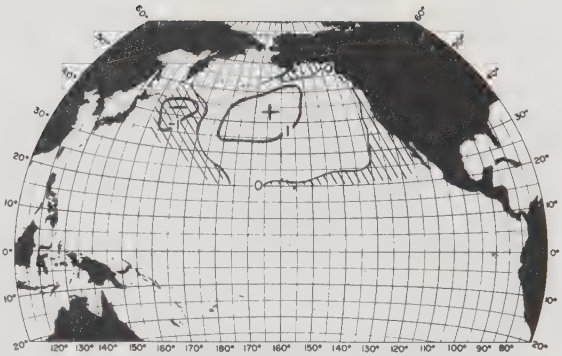

FIGURE 30.—Sea-surface temperature anomaly for September 1962. Hatched areas colder than normal. Heavy lines represent the 1° C anomaly contours which define warm (+) or cold (−) cells.

relative to the width of the current can create an anomaly of 1° C to 2° C. The amplitude of the perturbation in the current must, of course, be greater than that in the temperature field, since the water must adjust toward new equilibrium temperature appropriate to the local heat exchange processes as it changes latitude. Thus, a parcel of water following a northward deflection of the streamlines would arrive at the northern bend, or crest, of a standing wave with a temperature lower than it would have had if no deviation from zonal flow had occurred. Owing to the advective effect, it would nonetheless be warmer than an equivalent parcel of water reaching the same location by a normal, zonal trajectory.

The existence of a perturbation upstream from the location where the West Wind Drift splits may have a significant effect on the proportional flow into the Alaska Gyre and the California Current. For example, in a wave formed by a northward deflection of the zonal current, water moving downstream from the crest would have a southward component which might favor more transport into the California Current. A strengthening of this current would cause the isotherms to adjust to the effects of increased cold advection and local heat exchange processes southward of their normal positions, creating a negative anomaly. Correspondingly, the reduced northward transport would decrease warm advection into the Gulf of Alaska and the isotherms would adjust to equilibrium positions farther south than normal, also creating a cold anomaly.

If the northward deflection in the foregoing example is replaced by a southward deflection, then, after passing the southern bend or trough of the wave, the water would approach the coast with a northward component, favoring more transport into the Gulf of Alaska. The balance between advection and local heat exchange would be established with the isotherms north of their normal positions, creating a warm anomaly.

In a comprehensive treatment of oceanographic survey data taken in 1955-58, Tully, Dodimead, and Tabata (1960) found the warm coastal anomaly of 1957-58 to be associated with increasing transport into the Alaska Gyre. They describe this condition in terms of a southward shift of the point of separation of flow from the West Wind Drift. From their study of the dynamic topography, they inferred that prior to the shift, in 1955 and 1956, most of the water approaching the coast south of lat 45° N entered the California Current. The fact that negative anomalies prevailed along the coastal zone in the latter half of 1955 and, to a lesser extent, in 1956 suggests that the point of separation in this period was farther north than usual.

Whether the partition of the West Wind Drift is influenced by upstream perturbations in the zonal flow structure cannot be established with certainty from the available survey data. The geopotential topography as presented by Dodimead, Favorite, and Hirano (1963) for the years 1955-59 does not reveal conclusive evidence of upstream wave structure. The physical evidence is limited to the anomalous characteristics of the surface temperature field which have already been discussed.

Some added perspective might be gained by looking briefly at the dynamic constraints applicable to a standing wave in the West Wind Drift. The average eastward current speed, U, for a wave of length L and lateral (north-south) extent D is given by Panofsky (1956) as follows:

$$U - C = \frac{2\Omega \cos\phi L^2}{4\pi^2 E} \left(\frac{1}{1 + L^2/D^2}\right)$$

where C is the wave speed (zero for a standing wave)

ϕ is the mean latitude

Ω is the angular velocity of the earth (7.292×10^{-5} sec^{-1})

E is the radius of the earth (6.37×10^{6} m).

This expression reduces to the Rossby wave equation for a uniform zonal stream on a rotating planet when the value of D approaches infinity.

In order to evaluate the right side of the above equation, we will assume dimensional similarity between the inferred wave and areas enclosed by the plus or minus 1° C anomaly contours for those cases where we presume a causal relation with the current structure. Estimates of the wave length L and of the ratio L/D were determined from rough measurements of the longitudinal and lateral extent of the warm cell present from October 1961 to September 1962. Excluding two extreme cases (April and July 1962) the longitudinal dimensions of the warm cell ranged between about 800 (March 1962) and 1600 (January 1962) nautical miles. The corresponding ratios of longitudinal to lateral extent for these particular cases were 1.3 and 2.0 respectively. Substitution of these values for L and L/D in the wave equation yields 35 and 85 cm/sec (approximately) for average current speed through a stationary wave. Of course, the areas enclosed by the 1° C anomaly contours presumably define only a portion of the hypothetical wave, and to substitute the dimensions of these areas for L and D would understate the theoretical current speed.

Current speeds in the West Wind Drift, computed from dynamic height anomalies, are generally less than 10 cm/sec (Dodimead et al, 1963). Data from drift bottles (Dodimead and Hollister, 1962) indicate current speeds up to 20 cm/sec in the same region. Thus, the theoretically computed results are too high, but considering the approximations used they are not altogether unreasonable.

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Oil Pollution on Wake Island from the Tanker R. C. Stoner

By

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ABSTRACT

On September 6, 1967, the tanker R. C. Stoner foundered on the reef off the harbor entrance at Wake Island. During the following 10 days the vessel's cargo of over 22,000 kliters (6 million gal) of high octane aviation gasoline, aviation jet fuel, aviation turbine fuel, diesel oil, and bunker C black oil was spilled along the southern coast of the island.

A shore and underwater survey of the contaminated coastline showed that an estimated 2,500 kg of inshore reef fishes were killed and stranded on the shore. Numerous other fish and invertebrates were probably killed. Evidence is cited which indicates that most of the kill occurred on the shallow reef flat and the author speculates on the lethal effect of the various fuels.

INTRODUCTION

On September 6, 1967, the SS R. C. Stoner, an 18,000-ton tanker, went aground about 200 m southwest of the harbor entrance at Wake Island (Figures 1 and 2). She was in the process of mooring to two buoys located outside the harbor when the strong southwesterly wind drove her onto the reef.

When she foundered, the R. C. Stoner was loaded to capacity with over 22,000 kliters (6 million gal) of petroleum products. The cargo consisted of (1) 13,300 kliters (3,507,000 gal) of J-P4 military aviation jet fuel, a mixture of kerosene and gasoline which is light yellow and mixes readily with water; (2) 6,700 kliters (1,785,000 gal) of A-1 commercial aviation turbine fuel, a kerosene fuel which is light brown, mixes readily with water, and is a relatively safe fuel to handle; (3) 1,600 kliters (420,000 gal) of 115/145 aviation gasoline, a highly combustible fuel for high performance reciprocating engine aircraft, which is light purple and contains tetraethyl lead; (4) 640 kliters (168,000 gal) of diesel oil, which is light brown; and (5) 525 kliters (138,600 gal) of bunker C black oil, the vessel's engine fuel and least volatile of the petroleum products on board.

Ollie Custer and I, of the Bureau of Commercial Fisheries Biological Laboratory (now National Marine Fisheries Service Hawaii Area Fishery Research Center), Honolulu, arrived at Wake Island on September 13 to survey and assess the damage to marine fish, invertebrates, and birds caused by the petroleum spillage.

Wake Island, lat 19°18' N, long 166°36' E, lies about 300 miles north northwest of the northernmost of the Marshall Islands and is administered by the Federal Aviation Agency (FAA). It has a loran station operated by the Coast Guard and a Pacific Missile Range installation maintained by the Air Force. Wake consists of three islets forming an atoll enclosing a shallow lagoon. The total land area is about 6.5 km^2 with a maximum elevation of about 7 m. The atoll is about 7.2 km long northwest to southeast and about 3.2 km wide. The lagoon has an area of about 9.1 km^2 and a

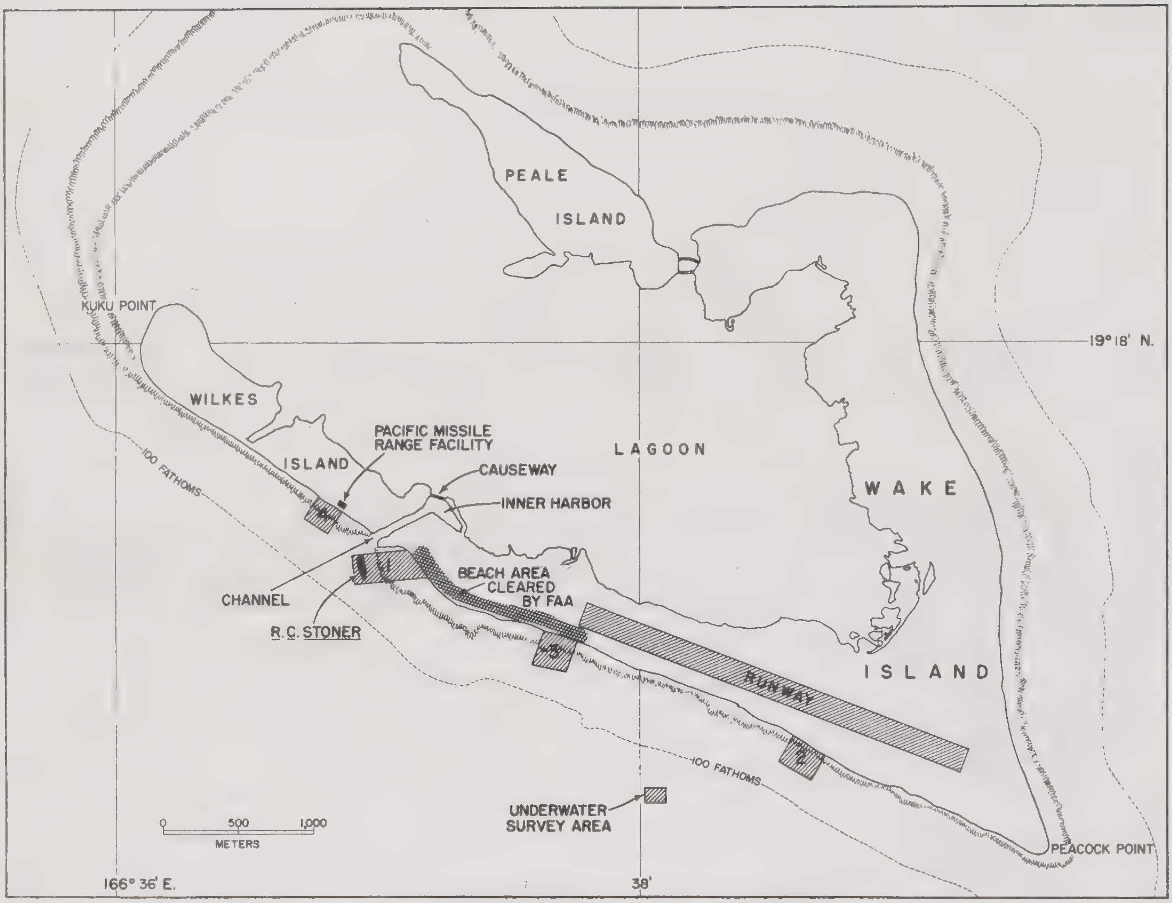

PEALE
ISLAND
KUKU POINT
19°18' N.
WILKES
ISLAND
PACIFIC MISSILE RANGE FACILITY
LAGOON
CAUSEWAY
INNER HARBOR
100 FATHOMS
WAKE
ISLAND
CHANNEL
R. C. STONER
BEACH AREA CLEARED BY FAA
RUNWAY
1
2
3
4
100 FATHOMS
UNDERWATER SURVEY AREA
0
500
1,000
METERS
166° 36' E.
38'
PEACOCK POINT

Figure 1.--Wake Island.

maximum depth of 3-4 m.

Immediately after the grounding, a large quantity of fuel spilled from the damaged tanks. It was believed to consist primarily of aviation gas, J-P4 jet fuel, and possibly A-1 turbine fuel. However, the following day bunker C fuel was also escaping in considerable quantity (Figure 3). Gasoline vapor could be smelled until September 9, but not subsequently, indicating that the vessel was clear of gasoline within the first few days.

Unsuccessful attempts to pull the *R. C. Stoner* from the reef with her cargo intact made it apparent that it would be necessary to lighten the vessel before salvage operations could proceed. However, continuing southwesterly winds and rough seas caused by the recent close passage of typhoon Opal and tropical storm Rita delayed salvage. Southwesterly winds of 18 to 25 knots continued until the morning of September 16.

On September 8, the stern section of the *R. C. Stoner* broke off and plans to float the vessel free were abandoned. During the first 3 days after the grounding, the prevailing southwesterly wind drove the escaping fuel into the small boat harbor and along the coast for about 4 km towards Peacock Point (Figure 1). It was estimated that as much as 2,285 kliters (600,000 gal) of mixed fuels covered the surface of the small boat harbor with a layer up to 20 cm thick (Figure 4). The volume of petroleum products washed up on the south coast was not estimated. Only small quantities of oil reached the shore on the Wilkes Island coast to the northwest of the harbor entrance and relatively few dead fish were seen stranded on that shore.

Large numbers of dead fish were stranded mostly along two high-water levels between the harbor entrance and Peacock Point. The odor of putrefying fish was strong as far as 3.2 km away. The intensity of the kill diminished

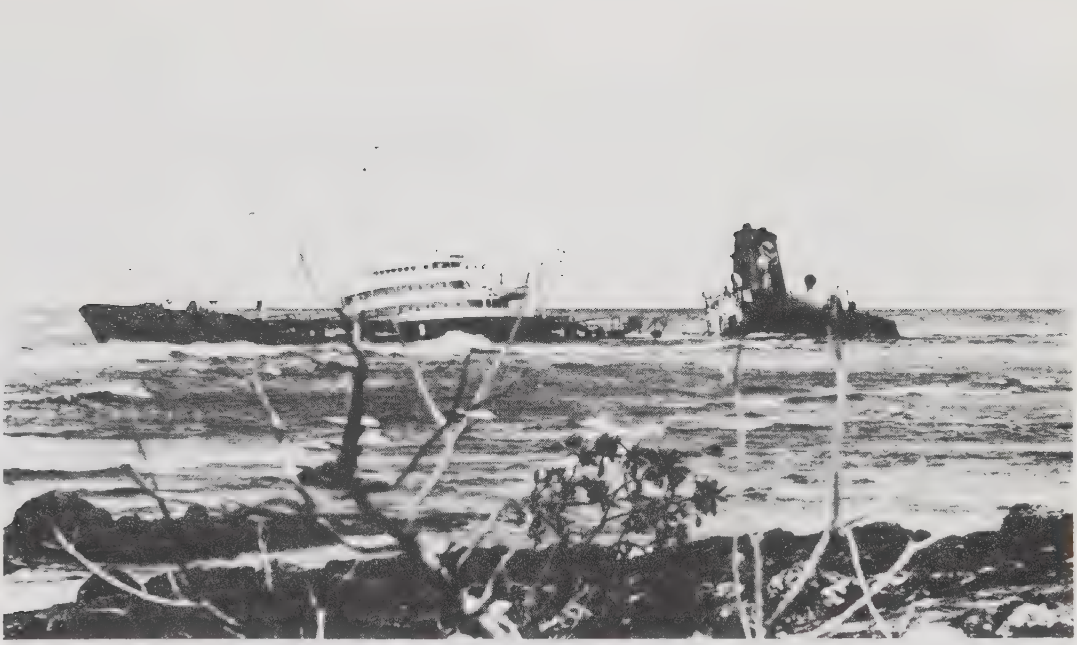


Figure 2.--R. C. Stoner, aground off the harbor entrance.

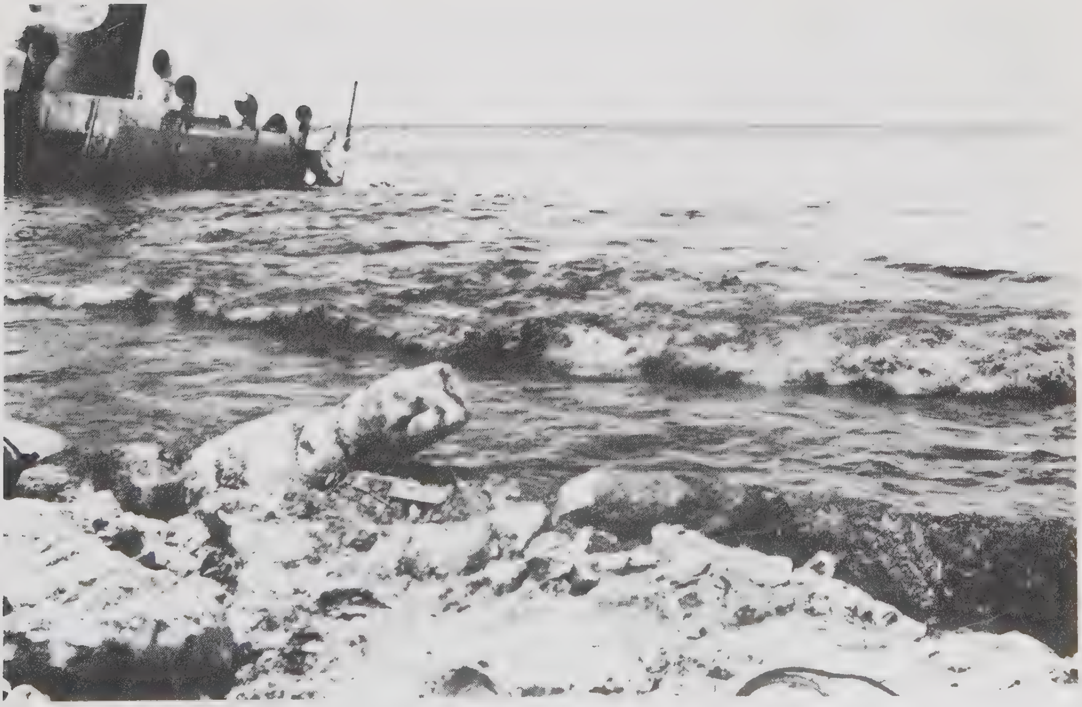


Figure 3.--Oil blackened surf.

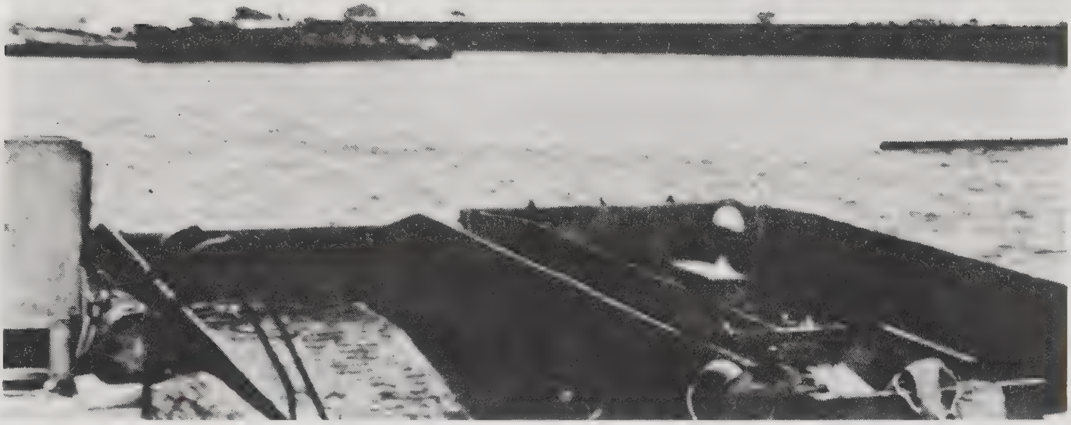


Figure 4.--Inner small boat harbor was covered with about 20 cm of oil.

along the shore towards Peacock Point. On the southern side of the point, few dead fish were seen, and no dead fish or shoreside petroleum pollution was seen on the northern side of the point.

On September 11 and 12, FAA personnel in cooperation with crewmen from the R. C. Stoner had cleared most of the larger fish from the shore area that had received the bulk of the dead fish. The cleared shoreline extended from the harbor entrance southeast for about 2,300 m (Figure 1).

By September 13, a U.S. Navy harbor clearance team had arrived from Subic Bay, Philippine Islands, to assist in removing the vessel. Two Navy tugs, a Navy salvage ship, the U.S. Conserver, a Navy tanker, the U.S. Noxubee, and USCG Mallow were laying offshore to assist in the salvage of the R. C. Stoner and her cargo.

Standard Oil Company and U.S. Navy personnel were removing oil products from the surface of the small boat harbor. Utilizing air-driven pumps and surface skimmers, they were pumping oil into pits dug close to the harbor. The oil in the pits was burned each evening. Over 100,000 gal were estimated to have been removed from the harbor and disposed of by this technique.

SHORELINE SURVEYS

We made spot surveys along the full length of the seaward and lagoon coastlines of the atoll to determine and assess the effects of the contamination.

The Lagoon

No petroleum products had entered the lagoon. The harbor is blocked from the lagoon by an earthen causeway which had prevented entry of oil into the lagoon from the harbor. The prevailing westerly winds and currents evidently prevented pollutants from entering the lagoon over the reef on the northwestern end of the atoll.

Area Cleared of Fish by the Federal Aviation Agency

With few exceptions all the larger fish had been removed from the cleaned section of the shoreline. The remaining small fish were concentrated in windrows along two oily high-water marks along the coastline. Both high-water lines were the result of abnormally high tides in combination with the strong onshore wind and high seas which prevailed early in September. They were about 8 and 3 m higher up the beach than the high-water level on September 13. The fish were usually thickly covered with oil. They consisted largely of pomacentrids (damselfishes) and acanthurids (surgeonfishes); Pomacentrus nigricans, Abudefduf sordidus, and Acanthurus triostegus seemed to predominate. We estimated that the remaining fish on this section of the coast probably did not amount to more than a few hundred kilograms.

Dead turbine molluscs, Turbo sp. (Figure 5), and dead sea urchins, Tripneustes sp., were abundant. We also saw a few dead beach crabs and small cowries.

Personnel involved in the fish cleanup oper-

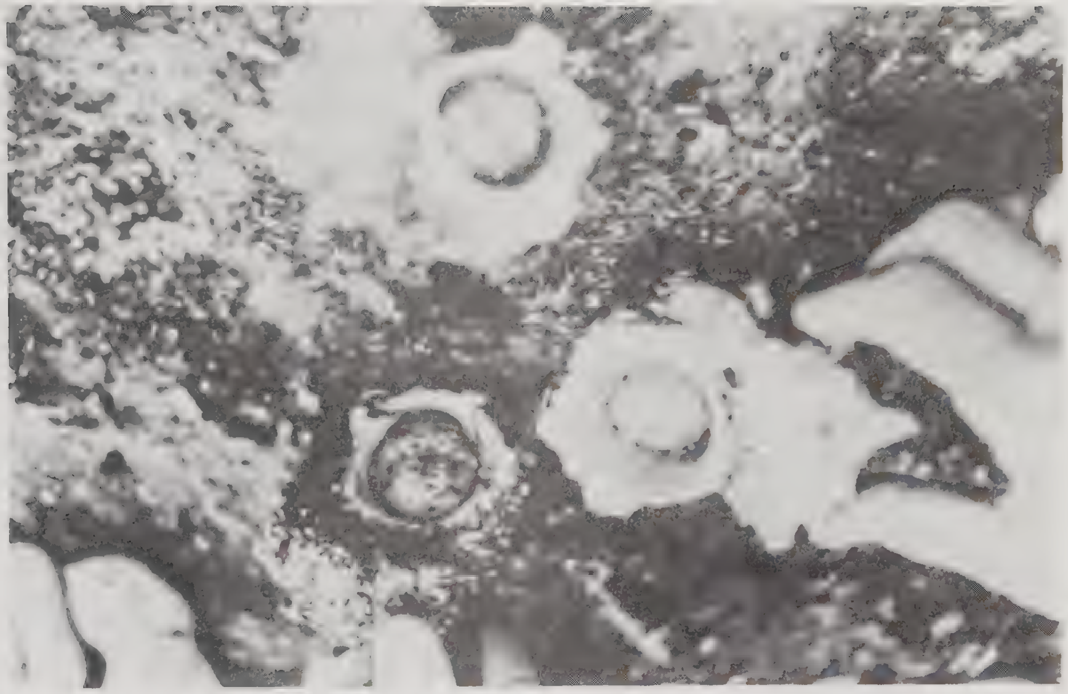


Figure 5.--*Turbo* sp. suffered high mortality.

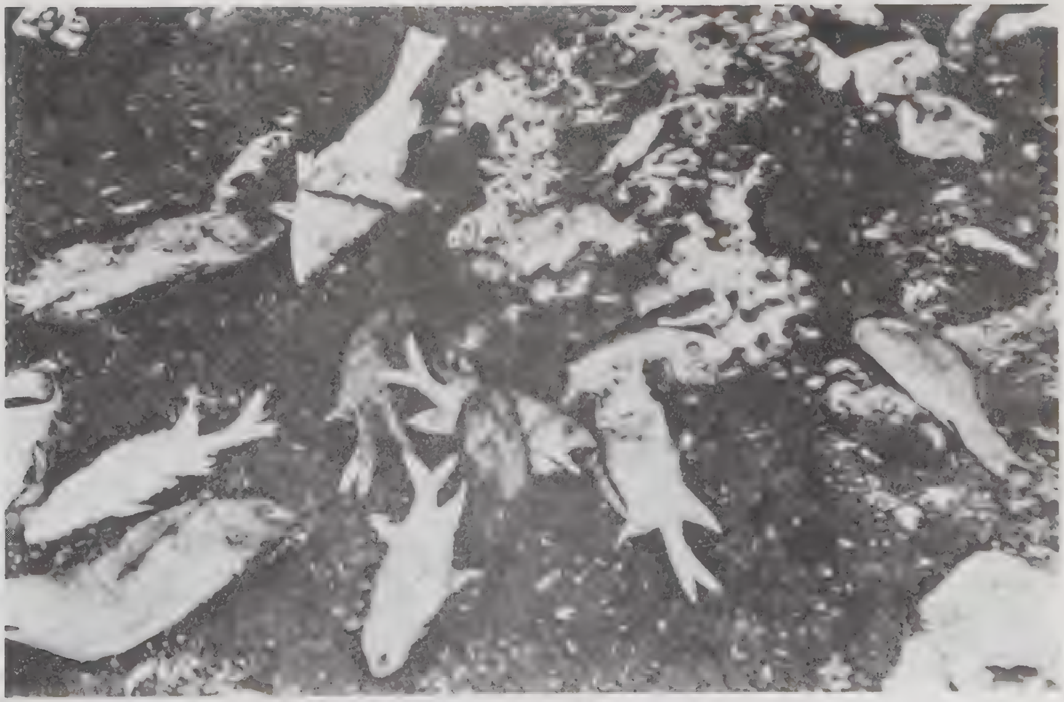


Figure 6.--Fishes stranded on the oil blackened beach.

ation had saved specimens of the various species they had collected. These were identified and photographed. Their records showed that approximately 1,360 kg of fish were collected during the cleanup. Based on their rough estimates, by number, 40% were surgeonfishes, mostly *Acanthurus triostegus* and *A. achilles*; 30% were parrotfishes; 10% were squirrelfish *Holocentrus lacteoguttatus*; and 20% were other species, many of which were groupers. Very few dead moray eels were collected during the cleanup.

They saw numerous dead sea urchins and turbine shells, but these had not been removed. A visit to the dump, where the fish had been disposed of, enabled us to verify some of the information supplied, relative to quantities and percentages.

Area Not Cleared by the Federal Aviation Agency

Oil contamination continued for about 2.4 km southeast of the section that had been cleaned. Here too, the majority of dead fish were well above normal high water. Some were even enmeshed in the branches of low bushes. We counted the larger fish (over approximately 15 cm), identified them, and took photographs (Figure 6). Table 1 lists the species we identified in the kill, including specimens saved by the cleanup crew. We did not attempt to identify the hundreds of small oil-covered specimens which no doubt included many additional species. Table 2 includes only the larger fish that were counted on the uncleared shore. The total weight of fish stranded on this section was probably not much over 900 kg.

The scarcity of moray eels was interesting. Local divers and fishermen said that morays were abundant on the reef, but only two dead moray eels were found. During the underwater surveys of the reef flat none were seen. The eels may have detected the pollution and fled the area before the concentration became lethal, or they may have survived it and were not seen.

We saw considerable numbers of dead turbine shells. No counts were made. Few sea urchins had been killed along this section compared with the more northwesterly shore. The only other dead invertebrates were occasional cowries, nudibranchs, and grapsoid crabs. Numerous hermit crabs were observed feeding on the dead fish, but we saw no dead hermit crabs.

The Small Boat Harbor

The small boat harbor was a trap for large quantities of the petroleum spillage. There was a layer of mixed fuels which at times was 20 cm deep in the inner part of the basin. The harbor banks were fouled with a thick layer of

Table 1.--Some of the fishes washed up on the south coast of Wake Island, east of the wreck of *R. C. Stoner*.

- Serranidae (groupers)
    - *Cephalopholis argus*
    - At least two other unidentified species
- Holocentridae (squirrelfish)
    - *Holocentrus lacteoguttatus*
- Scaridae (parrotfishes)
    - *Scarus perspicillatus*
    - *Scarus sordidus*
    - At least two other unidentified species
- Mullidae (goatfish)
    - Unidentified
- Acanthuridae (surgeonfishes)
    - *Acanthurus achilles*
    - *Acanthurus nigricans*
    - *Acanthurus triostegus*
    - *Ctenochaetus striatus*
    - *Zebrasoma flavescens*
    - *Zebrasoma veliferum*
- Chaetodontidae (butterflyfishes)
    - *Centropyge flammeus*
    - *Chaetodon lunula*
    - *Chaetodon semeion*
- Balistidae (triggerfishes)
    - *Melichthys vidua*
    - *Rhinecanthus rectangulus*
- Scorpaenidae (scorpionfish)
    - *Pterois volitans*
- Diodontidae (puffer)
    - *Diodon hystrix*
- Muraenidae (moray)
    - Unidentified
- Mugilidae (mullets)
    - Unidentified
- Pomacentridae (damselfishes)
    - *Abudefduf imparipennis*
    - *Abudefduf sordidus*
    - *Pomacentrus nigricans*
- Priacanthidae (bigeye scad)
    - One specimen found--unidentified
- Cirrhitidae (hawkfish)
    - Unidentified
- Carangidae (jack)
    - Unidentified
- Labridae (wrasse)
    - *Thalassoma umbrostigma*

Table 2.--Fishes (>ca. 15 cm) counted on the shoreline which had not been cleared by the FAA

Family	Count	Percentage of total number	Percentage of total estimated weight
Holocentridae (squirrelfishes)	384	37	9.5
Acanthuridae (surgeonfishes)	288	27.4	7.6
Scaridae (parrotfishes)	284	27.4	59.9
Serranidae (groupers)	52	5.0	21.0
Balistidae (triggerfishes)	20	2.0	1.0
Scorpaenidae (scorpionfishes)	8	0.6	0.2
Mullidae (goatfishes)	4	0.3	0.1
Diodontidae (spiny puffers)	4	0.3	0.2
Muraenidae (morays)	2	0.1	0.1

black bunker fuel. A survey of the kill along the perimeters of the channel and inner harbor revealed considerable numbers of small fish, very few large fish, numerous grapsoid crabs, and some small sea snakes; most of these were heavily fouled with black oil. The fish included various pomacentrids, small scarids (parrotfishes), and acanthurids. Although the fish were numerous, the total biomass of the kill was relatively small, probably only a few hundred kilograms. We learned from FAA personnel who worked around the docks that the fish population in the harbor was normally sparse. The heavy layer of oil on the surface and emulsified jet fuel below precluded diving in the channel or harbor; however, survival of marine vertebrates and invertebrates seemed unlikely under such intense contamination.

Sea Birds

Hundreds of thousands of sooty terns were aggregated in the air to the northwest of Wilkes and Peale Islands (Figure 7); frigate birds in considerable numbers and a relatively few shearwaters were also present. The birds were concentrated over areas which did not

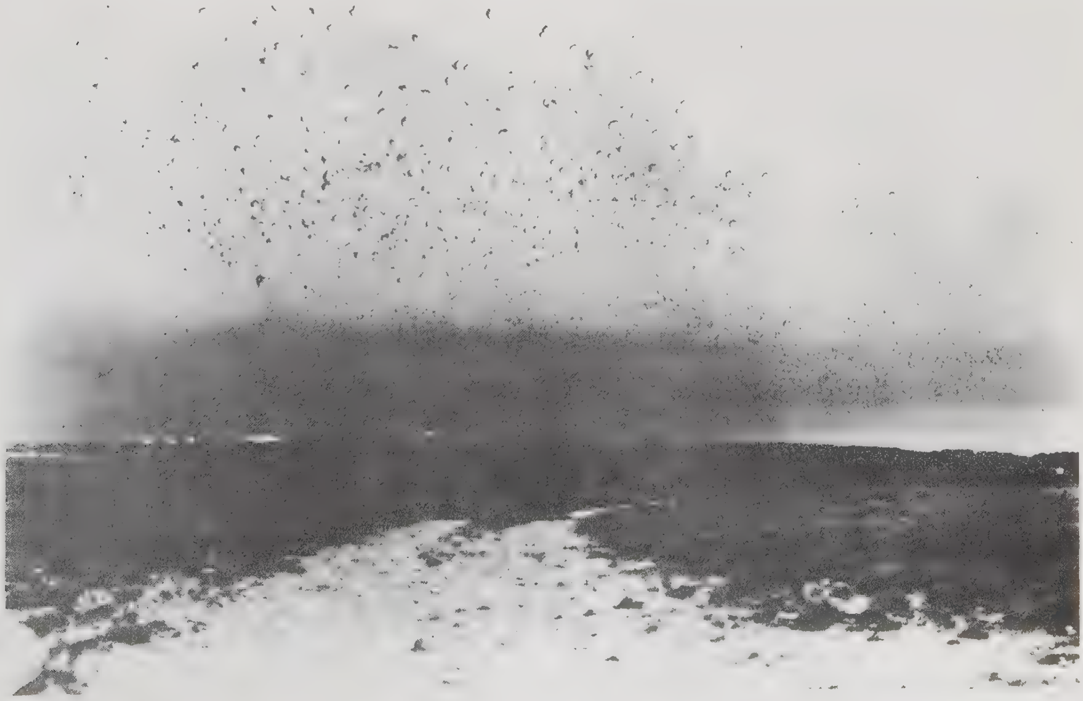


Figure 7.--Large aggregations of sooty terns off the western end of the island.

receive petroleum spillage. No birds were seen along the fouled coastline. There was no indication that any bird life on the atoll had been killed or harmed by the spill.

UNDERWATER SURVEYS

Underwater surveys were made (1) in the vicinity of the R. C. Stoner, (2) 2.5 km southeast of the harbor entrance, (3) on the reef flats and reef fronts about 1 km southeast of the harbor entrance, and (4) on Wilkes Island about 300 to 400 m northwest of the R. C. Stoner (Figure 1). Dives were also made in the lagoon and in uncontaminated areas along the northwesterly reefs. The lagoon supports a large population of fish. Had large quantities of petroleum products entered this shallow enclosed area mortality would probably have been very high. No dead fish were seen in the water at any of these places.

The Vicinity of the Wreck

During survey 1 the ocean around the R. C. Stoner contained a considerable amount of what was probably jet fuel that had emulsified with the water which was a dirty straw color to a depth of 7 m or more. This contamination was sufficient to cause skin irritation and after an hour we were covered with a light oily film and were in much discomfort. Itching and tenderness of the skin in the more sensitive areas persisted for several days.

Many fish were seen on the reef around the wreck. Most of them were on the bottom (10-12 m) where the water was less contaminated. Many were within 2-3 m of the ship. Curiously, we saw numerous individuals of the leatherback runner, Chorinemus sanctipetri (Figure 8), frequently come up and swim around in the upper 3 m of water where the pollution was heaviest. At the after end of the vessel the water was so contaminated that we dared not swim around the stern. In spite of this, we saw leatherback runners swimming in this area, with no apparent ill effects. We thought that the combination of irritation and oiliness would have a deleterious effect, particularly on the gills. However, individual fish may have remained in the contaminated water for brief periods only.

The coral heads immediately seaward of the wreck and from 3 to 15 m from it were well populated with fish. These included parrot-

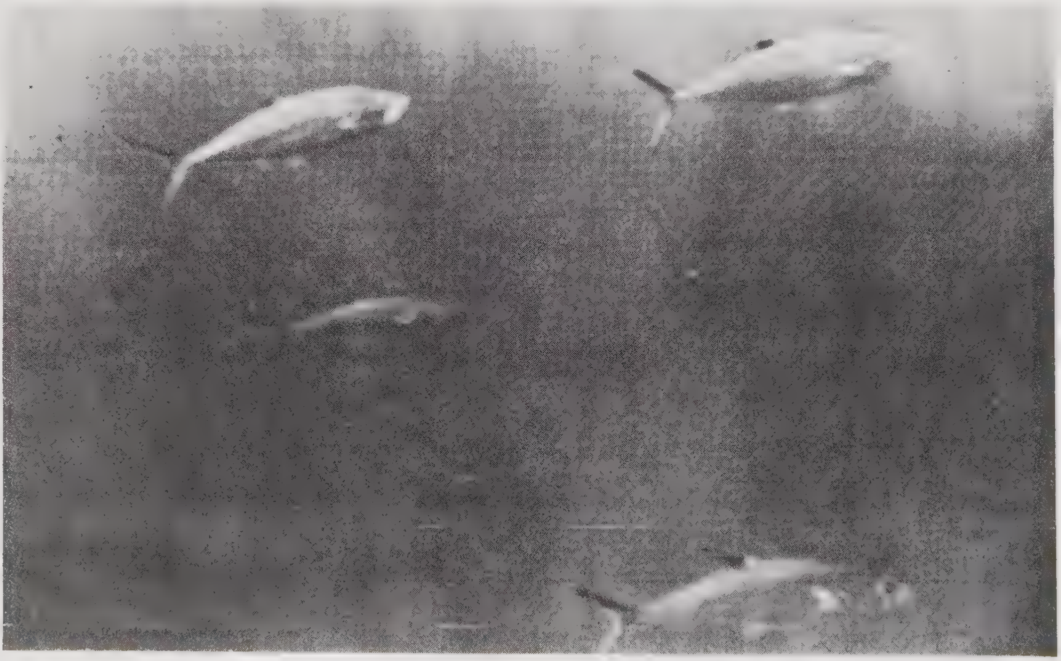


Figure 8.--Leatherback runners, Chorinemus sanctipetri, swimming in an area heavily contaminated with jet fuel.

fishes (Scarus perspicillatus, Chlorurus gibbus, and at least two other species, probably S. sordidus and S. brunneus), surgeonfishes (Acanthurus triostegus, A. achilles, A. nigricans, and A. guttatus), butterflyfishes (Chaetodon setifer, C. auriga, C. lunula, C. quadrimaculatus, and Forcipiger longirostris), grouper (probably Cephalopholis argus), porgy (Monotaxis graduculis), wrasse (Thallassoma umbrostigma), triggerfishes (Melichthys vidua and M. buniva), puffers (probably Diodon hystrix and Arothron meleagris), damselfishes (Pomacentrus nigricans and Dascyllus aruanus), and squirrelfish (probably Holocentrus lacteoguttatus). Two unidentified species of jacks (Carangidae) were numerous.

Although there were numerous fish around the reefs close to the ship, we later found, after subsequent dives, that other areas on the reef front farther away from the source of pollution were more densely populated than the reef front near the R. C. Stoner. During the period of greatest petroleum spillage, many fish in the wreck area were probably either killed or driven away.

The reef flat directly inshore of the wrecked ship is about 0.5 to 2 m deep at low tide and about 125 m wide, the widest such area on this coast. We found it nearly barren of fish. The bottom is flat, covered with coralline rubble with few coral heads. One would not expect such a reef normally to support a very large population of fishes, but neither would it be expected to be as depauperate as it was. Probably, many of the fish in this area had been either killed or driven off.

Sea Off Wake Island Between the Harbor and Peacock Point

Time and weather permitted us to make two underwater surveys off this coast (surveys 2 and 3, Figure 1). Both surveys were made in areas where considerable numbers of fish had been stranded on the shore.

On September 15, the wind was still strong from the southwest. A heavy sea was breaking on the reef 2.5 km southeast of the harbor, where we made survey 2. Weather reports indicated that typhoon Sarah would pass very close to Wake in about 48 hr and sea conditions were poor for diving. However, we decided it would be best to survey the polluted coast outside the reef as best we could before the typhoon arrived. We were unable to find any passes through the reef so scuba was not used.

The heavy turbulence on the reef flat made visibility poor. The reef flat there is about 30 m wide and has numerous coral formations. It should support a substantial fish population; however, we saw relatively few fish. The dominant groups were various scarids (not including adult humpback parrotfish, C. gibbus), and acanthurids, the latter mostly A. triostegus and A. achilles. We saw no grouper or squirrelfish. There was no petroleum or dead fish in the water. At least part of the sparsity of fish on the shelf was probably due to the heavy seas.

The reef front drops off steeply to a depth of about 8 m. Visibility was better than on the flat. There were numerous rock and coral formations and a myriad of fish. Time did not allow us to obtain any data on the density of the fish population on the seaward side of the reef. However, on the basis of past experience, we considered the population to be high. This population included a wide range of the common reef groups. The most numerous species were generally the same ones that were the most plentiful in the kill: several species of parrotfishes; surgeonfishes, predominantly A. triostegus and A. achilles; several species of groupers, mostly C. argus, and various pomacentrids and chaetodontids. Exceptions were squirrelfish, few of which were seen, and adult humphead parrotfish, which was numerous outside the reef but apparently absent in the kill.

Shortly after crossing the reef, we encountered numerous blacktip sharks, Carcharhinus melanopterus. During this survey and subsequent surveys outside the reef, we were frequently pestered by sharks, most of them 1.2 to 1.5 m long. They were extremely curious and persisted in making close passes, frequently coming within less than 1 m of us. They were remarkably bold and did not scare easily. Local skindivers considered the abundance and boldness of the blacktips as very unusual. The only way we can account for their concentration and behavior is that the sharks had been attracted to the area by dead fish and had become conditioned to finding abundant food drifting around. Such conditioning might result in immediate attack behavior, without the preliminary investigation usually more characteristic of sharks. The behavior of the sharks was a little disconcerting and hindered us somewhat, as we had to keep a constant watch in order to chase them off. It is interesting to note that no shark was reported in the kill.

We covered about 275 m of coastline. As on the reef flat we saw no dead fish or invertebrates, nor any indication of petroleum in the water.

We made survey 3 off the south coast about 1.7 km southeast of the wreck (Figure 1) on September 16. The wind had abated and the sea was the calmest we had seen since our arrival. The heaviest beach-stranded kill had occurred in this general area. We surveyed the reef flat for about 125 m. The reef in this area was similar to that in survey area 2, but the fish population, dominated by Scarus sordidus, Acanthurus triostegus, A. achilles, and Ctenochaetus striatus, was larger. We saw no squirrelfish, grouper, or adult humphead parrotfish on the reef flat. The reef front dropped off abruptly to about 8 m. We were again impressed by the abundance of fish life, which was far greater than on the reef flat. Here also, parrotfishes and surgeonfishes dominated. We saw several different species of Scarus and numerous large C. gibbus; in addition, C. argus and at least three other species of groupers and two species of carangids were plentiful. We saw a number of squirrelfish, which appeared to be the same species, H. lacteoguttatus, which occurred in the kill. As in survey 2, we saw most of the species that were in the kill, plus many more. Those species which were most abundant in the kill were apparently also the most abundant offshore. Humphead parrotfish and squirrelfish were exceptions. We encountered numerous blacktip sharks behaving in the same manner as on the previous day.

Sea Off Southeastern End of Wilkes Island

The area in front of the Pacific Missile Range facility about 300 to 400 m northwest of the R. C. Stoner was chosen for survey 4 (Figure 1). Because of the prevailing southwesterly winds and possibly the current, very little oil had washed up there, but instead had been driven up the channel into the inner harbor. On our survey of the beach on Wilkes Island, we had found little oil and few dead fish. Because that area had apparently been relatively little affected, we thought it would serve as a useful comparison to the two more easterly surveys. Local scuba divers told us it was one of their favorite diving spots, and that there were many fish on the reef front and sharks were rare. Curiously, during our brief survey, we found neither the reef flat nor the reef front nearly as abundant in fish as the previously investigated areas; we saw few parrotfishes and no dead fish in the water, but we were bothered by blacktip sharks and later by two larger (2.0-2.5 m) gray sharks. The latter, which we could not positively identify as to species, manifested the same aggressive tendencies as the blacktips, making very close passes. We were a bit more leery of large sharks with this type of behavior and left the area posthaste.

CONCLUSIONS

By noon of September 16, large storm seas were rapidly building up on the reefs and it was impossible to continue the survey. That night typhoon Sarah struck Wake with winds up to 67 m per sec (140 miles per hr) causing great damage to the island's facilities. The typhoon, however, had one saving grace: it blew away virtually all of the oil that had accumulated in the inner harbor and even did a good job of scouring its oil-fouled banks, solving in one night a problem which would have taken many weeks to overcome. On the morning of September 17, the harbor was clear and clean. A brief survey of the affected beach areas disclosed that the only remaining evidence of pollution was black oil embedded in reef flat crevices and impregnated in coral. The authorities on the island were evacuating all nonessential personnel because of an acute housing shortage. Thus, we were unable to make an underwater survey of the now oil-free inner harbor. This was unfortunate. Even though we have no ''before pollution'' data on the harbor, it would have been of great value to have an accurate assessment of the biological conditions of a shallow confined area of this nature, the surface of which was completely covered with a thick film of heavy oil and the subsurface contaminated with light fuel for over a week.

We estimate that about 2,500 kg of dead fish were washed up on the south shore during the period of maximum petroleum escapement, the first week after the R. C. Stoner had foundered. Our best guess is that most of the kill had occurred on the shallow reef flat bordering the coast. The available evidence appears to support this theory. Numerous groupers and squirrelfish occurred in the kill. Apparently, all of the squirrelfish were H. lacteoguttatus and nearly all the groupers were C. argus. We saw neither of these groups on any of the reef shelves we surveyed, yet they are generally the most abundant of their respective families occurring in shallow water around Wake. C. argus were frequently observed outside the reef. We saw few H. lacteoguttatus outside the reef; however, as with the eels, assessment of a squirrelfish population in the daytime by visual means is impossible, especially without using scuba. Groupers and squirrelfish on the reef shelf may have holed up when they sensed the pollution, rather than escaping to uncontaminated water outside the reef. Thus, they would be very vulnerable and suffer exceptionally high mortality. As far as we could determine, no adult humphead parrotfish, C. gibbus, was killed. Adults of this species were not seen on the reef shelves that had been polluted nor in unpolluted shallow areas but were numerous outside the reef. It is possible that young C. gibbus were among the kill and not detected. C. gibbus does not develop the enlarged forehead characteristic of the adult until it is quite large. During the survey we were not familiar with the appearance of the young fish. Other species of parrotfish (these may have included young C. gibbus) were apparently very vulnerable to the petroleum pollutants. If one assumes that adult C. gibbus were also vulnerable, lethal pollution probably did not extend into the deeper water outside the reef.

It is interesting to speculate as to which of the various fuels caused the most mortality. Within an hour after the grounding it was known that aviation gasoline was escaping because its distinctive smell permeated the area and eventually spread over most of the island to leeward of the vessel. However, concurrently with the gasoline, J-P4 jet fuel and possibly A-1 turbine fuel were leaking. There is no record of the extent of fish mortality or even if any mortality had occurred the day the ship grounded. The morning after the grounding (September 7), black fuel oil was leaking in large amounts and gross black oil pollution extended along the shoreline and into the small boat harbor. Dead and dying fish were first noted on September 7. On September 8 there was an extensive fish kill along the beach. All of the aviation gasoline had apparently spilled by the morning of September 9 as the presence of gasoline vapor in the air could no longer be detected. A large part of the black oil had also spilled by September 9, but the remainder continued to escape at least through September 15. Large quantities of aviation jet fuel, aviation turbine fuel, and possibly diesel fuel were escaping through September 16. However, there was no evidence of fish mortality subsequent to September 10.

Near the wreck we observed that numerous reef fishes and leatherback runners showed a surprising tolerance to jet fuel or turbine fuel, or both. The seaward side of the reef, below the surface, was probably contaminated only with light fuels, including aviation gasoline, whereas the reef flat received both light fuels and black oil mixed into the water by the heavy surf.

Although admittedly poorly documented, the evidence indicates that the petroleum product most lethal to fish was either aviation gasoline (which contains tetraethyl lead, a known toxic agent) or black oil. Other oil spillages have indicated that fish are not seriously affected by crude oil, which is primarily confined to the surface. Laboratory experiments have corroborated this finding. However, when a large volume of heavy oil is well churned onto a shallow reef flat, the mortality may be expected to be high.

Considerable numbers of fish must have been killed on the reef flat and washed out into deep water; however, we were unable to estimate the percentage of the kill that did not wash ashore. By September 13, when we started our investigation, fish apparently were not being affected by oil pollution. We saw neither dead fish in the water nor any fish showing signs of distress.

We made only cursory observations on the invertebrates. The turbinid snails and sea urchins were the only animals found dead in large numbers. The population of Turbo on the south coast of Wake may have been seriously depleted. Damage to many of the various small invertebrates commonly inhabiting coral reefs may have been severe. These invertebrates have the slowest recovery rate and thus their depletion would have the most profound effect on the ecosystem of the reef flat.

We observed that the fish population on the reef front and slope was dense. This proximal population would provide a source for rapid recruitment to both the reef flat and the inner harbor.

That the fish kill was negligible when compared with the surviving population may be attributed to three main factors. First, the nature of the coastal terrain was a saving factor, composed as it is of a narrow reef flat with the water depth dropping off rapidly along the reef front. Places with great expanses of shallow tidal area are far more vulnerable to any type of contamination. Secondly, the fact that oil was unable to pass from the inner harbor to the lagoon. Wake Island, of course, does have a relatively shallow area in the lagoon vulnerable to contamination. Had the heavy concentration of fuels which accumulated in the harbor entered the lagoon, a near "total kill" with long-lasting effects probably would have occurred. Third, a large percentage of the spillage entered and was trapped in the small boat harbor where it could do relatively little damage to marine life. Had this oil been able to spread along the outside reefs, the kill would have been greater.

After the typhoon a Navy salvage team found that the wreck had broken into three sections. All her tank tops were open to the sea and apparently all of her cargo had been removed by sea action.

The portion of the wreck remaining above water was considered hazardous to the instrument landing system on the runways, so the wreck was flattened to the waterline with explosives. During the course of the demolition operation there was minor weeping of petroleum products that formed a slick extending about 1.5 km offshore. With northeasterly trade winds prevailing there was no more shoreline pollution.

Poor weather and shortage of the time limited the scope of this survey, but the major shortcomings of the investigation were that we arrived too late to get the full picture of the damage, and that we had no clear concept of the normal pre-pollution situation in the areas we surveyed. We suggest that if at least two trained teams of biologists, including specialists in fish and invertebrates, were located at suitable laboratories on the Pacific and Atlantic Oceans, we could enhance our knowledge of the effects of oil pollution more efficiently. The teams would have suitable survey equipment readily available and could be dispatched immediately to any area where a petroleum pollution threat is anticipated or already exists. If possible, the group would reach the scene in time to survey the environment and biota before the oil arrives.

7107

Development and Testing of the Hybrid Tuna Purse Seine

Mise au point et essais de la seine coulissante hybride a thon

Les échecs observés dans un pourcentage élevé des coups de seines à thon effectués par les Américains sont à l'origine du projet d'étude d'une seine coulissante à thon expérimentale. La mise au point du projet a été réalisée au moyen de modèles à l'échelle. La fabrication et les essais en grandeur réelle de la seine sont décrits. Ce filet diffère des seines à thon américaines classiques sur les points suivants: (1) alèze plus légère, (2) coefficient d'armement plus faible, (3) ailes d'extrémités coupées en diminution, (4) assemblage des bandes de fond avec reprises de mailles progressives, (5) ralingues de flotteurs et de plombs d'égale longueur, (6) anneaux de boursage en bout du filet et (7) fixation des anneaux de coulisse en retrait des extrémités. Cette combinaison fournit une seine qui plonge plus vite, pêche plus profondément, et présente une meilleure configuration générale que les seines à thon classiques. On est venu à bout des difficultés apparues dans la manoeuvre et dans le sauvetage des dauphins capturés avec les thons en éliminant la particularité d'assemblage avec reprises de mailles.

Construcción y ensayo de una red de cerco hibrida para la pesca del atun

Un porcentaje elevado de los lances efectuados en la pesqueria de atún norteamericana con redes de cerco de jareta no tiene éxito. Esto indujo a realizar un proyecto experimental con redes atuneras de cerco de jareta. El desarrollo del diseño se efectuó mediante el empleo de modelos a escala reducida. Se describe la construcción y ensayo de redes de cerco de tamaño natural. Estas redes de cerco se diferencian de las que normalmente se fabrican para tal fin en los Estados Unidos enque tienen: (1) paños más ligeros; (2) un menor coeficiente de armadura; (3) los extremos de las alas en disminución; (4) incremento de la armadura con el empleo de cadenetas inferiores que van en disminución; (5) relinguas superior e interior de iqual longitud; (6) anillas en los extremos; (7) las anillas principales de la jareta colocadas en los extremos de la red. Esta combinación produce una red de cerco que se sumerge con más rapidez, pesca a mayor profundidad y da una mejor configuración total que las redes de cerco normales para pescar atún. Las dificultades que supone su manejo y la recogida de las marsopas capturadas junto con los atunes se resolvieron eliminando el empleo de cadenetas reducidas. Los ensayos de pesca indicaron que aumentaran las posibilidades de éxito utilizando esta nueva red de cerco.

COMPARATIVELY little technological research has been done on purse seines despite the fact that they take increasingly larger portions of the world's catch of fish. Observed differences in performance and construction of existing purse seines and rates of success (percentage of sets catching at least ½ ton) of purse seine sets for tuna in the eastern tropical Pacific Ocean as low as 50 to 60 per cent led to a project to improve the design of these tuna purse seines (Ben-Yami and Green, 1968). This project is here summarized.

DESIGNING HYBRID PURSE SEINE

It was decided to work on a seine design intended for "school fish", as opposed to one intended for tuna associated with porpoise ("Porpoise" refers to tuna associated with porpoise (Perrin, 1969) as opposed to pure schools of tuna. In porpoise fishing, the net is set on a porpoise school for the tuna found beneath them. If the set is successful, the problem is then to separate porpoise from tuna).

The experimental phase of the study (Ben-Yami and Green, 1968) consisted of testing two model purse seines underwater. The first, Model I, was a 1:25 scale model of the standard California tuna purse seine. After testing, it was reworked to form Model II in an effort to produce a better combination of performance characteristics. This experimental approach was based on the assumption that should two different seines be scaled down in a uniform manner, the main differences in performance between the models would parallel those between the full-scale nets. In Model II, the main alteration consisted of varying hanging coefficients (k_h) (hanging coefficient k_h: ratio of stretched length of adjacent sections of webbing or ratio of length of line to stretched length of adjacent webbing (Ben-Yami, 1959)), from 0.7 at the top to 0.9 at the bottom (see Table 1), introducing gavels (vertical lines at the net ends, which can be pursed separately), and tapering the body. Total size, ballast and other common components were not changed.

TABLE 1. CONVERSION OF HANGING COEFFICIENT (k_h) TO "HANG-IN" PERCENTAGE

k_h	*Hang in* (%)
0.62	60
0.7	43
0.75	33
0.78	28
0.79	27
0.8	25
0.83	20
0.85	18
0.86	16
0.87	15
0.9	11
0.91	10

Comparative tests indicated that Model II sank at twice the rate of Model I and offered a smaller escape opening at its ends while retaining the acceptable pursing performance of Model I. In addition, the working depth was less sensitive to horizontal strains observed on the netting in Model II than in Model I.

Results indicate that k_h is probably the most important design variable affecting sinking speed, area encircled, and pursing performance. Low k_h allows a faster sinking rate and greater area of encirclement during later stages of the set. It also causes the leadline to rise earlier during pursing. High k_h gives the opposite effects. Many other factors affect these and other performance characteristics such as weight of ballast, size of mesh, and size of twine.

The above mentioned factors were considered in the final design and manufacture of a hybrid purse seine, which essentially is a scaled-up Model II combined with design features from various other purse seine types.

HYBRID TUNA PURSE SEINE IN COMPARISON WITH U.S. TUNA PURSE SEINE

The main features of the hybrid seine which differentiate it from existing U.S. tuna seines are:

1. Lighter netting
2. Low k_h
3. Tapering of the lower four strips of netting
4. Incremental "hang-in" in the lower four strips
5. Floatline and leadline equal in length
6. Gavels or "breastlines" used at both ends
7. No main rings or bridles connected to the first and last 35 fm of seine.

Lighter Netting

The typical U.S. tuna seine is made up of seven or eight strips, each 100 meshes deep (MD) laced in horizontally, which extend full depth to the extreme ends of the seine. The ends are then baited to a short, 125 mesh long by 15 MD, border, which in turn is laced to a metal triangle. No tapers are used (fig 1, McNeely, 1961).

The hybrid seine (fig 2) was constructed of 100 per cent nylon netting of knotless braided construction. The main body of netting was laced into horizontal, 100 MD strips, except for the two bunts, which were laced in vertically to attain the maximum strength. Strength is needed at that point, as the maximum strain occurs there when drying the bunt prior to brailing. The maximum strength is achieved "with the run" (longitudinal) in knotless netting, which is opposite of that in knotted netting.

The top and bottom borders are 5 in. stretched mesh (M) 10-$\frac{1}{2}$ MD #54 (4,022 Tex) nylon netting and 5 in. M, 10-$\frac{1}{2}$ MD, #72 (5,512 Tex) nylon netting is used in the gavels at the extreme ends. Twine sizes were increased to #36 (2,706 Tex) and #42 (3,543 Tex) in the 100 fm (183 m) forward of the bunts (rolling strips). The top strip is #36 (2,706 Tex) because this is the area of greatest wear. The four strips in the bottom portion were reduced to #24 (1,984 Tex) twine. The centre bunt is #54 (4,022 Tex) and the main bunt is #60 (4,377 Tex). The netting requirements were planned with the idea of keeping the twine sizes as light as possible, while strengthening the areas of greater strain such as the perimeters and the rolling strips adjacent to the bunts.

Netting twine presently used in conventional tuna seines is rarely lighter than #42 (3,543 Tex) except in the rolling strips, where #54, #60, and #72 (4,022, 4,377, and 5,512 Tex) are used. The bunts and border strips are made up of #84, #96, and #120 (7,440, 9,921, and 11,023 Tex) nylon. The twine sizes used depend on vessel size and its ability to handle bulk and weight and stacking space available.

The lightness of netting and the mesh sizes, together with the weight of leadline, play a direct role in the sink rate of the seine. Thus, to enhance the sink rate the seine should be constructed of the lightest netting possible.

Lower k_h and Tapers

Standard tuna seines are hung using a k_h of 0.87 to 0.91. The k_h used depends on individual preference and varies from vessel to vessel. The body strips are usually laced together at k_h 1 except the seams which are laced to the float and leadline border strips. A common practice is to lace one or two meshes of extra netting every 2 fm to the border strips. This is done primarily because it is assumed that the heavier border strips shrink slightly more than the adjacent lighter strips. Should this premise be true, then the lacing ratio of all seams after shrinkage should be about 1:1.

The hybrid seine (fig 2) was hung at a k_h of 0.85 for the first 35 fm (64 m) at each end, followed by $k_h = 0.80$ for the next 15 fm (27 m). The extra tightness in the ends takes some of the strain from the leadline and floatline and allows easier hauling. The centre portion was hung at $k_h = 0.75$ with the exception of the centre bunt, which was 0.78. This was done to cut down undue bagging at the bunt, thus making it easier to "dry up" the seine for brailing.

The lower four strips (100 MD each) of the hybrid seine were started and ended with two bar, one mesh tapers (fig 2). Each taper was approximately 10.5 fm (19.2 m) long graduating from one mesh to 100 MD over this span. This deepened the hybrid seine by 400 meshes over a taper span of 42 fm (77 m) on each end. These tapers worked extremely well and are considered one of the best features of the new seine. Tapers eliminate unnecessary accumulations of netting at the ends of the seine as well as enabling maximum fishing depths precisely where they are most needed. The elimination of netting at the ends is also a great aid to drying up the catch prior to brailing. For further discussion of tapers the reader is referred to Jurkovich (1967).

An incremental "hang-in" was used in the lower four strips (100 MD) of the hybrid seine. The fifth strip was laced to the sixth strip at the rate of 30 meshes of the bottom of the fifth strip to 29 meshes of the top of the sixth strip (fig 2). The other lower strips were laced together in the same manner. This resulted in a progressive .967 reduction in each of the lower four strips which in turn reduced the k_h at the leadline to approximately 0.86.

Float- and leadlines

The hybrid seine was hung to a chain leadline 450 fm (823 m) long. This leadline was made up of 105 fm (192 m) of $\frac{3}{8}$ in (9.5 mm) dia galvanized proof coil chain at each end adjoining two 92 fm (168 m) pieces of $\frac{7}{16}$ in (11.1 mm) dia chain with 66 fm (121 m) of $\frac{1}{2}$ in (12.7 mm) chain in the centre portion (fig 3).

The floatline was also 450 fm (823 m) long. Its centre was $\frac{5}{8}$ in (15.9 mm) dia, three strand nylon rope 374 fm (684 m) long spliced to two 26 fm (48 m) pieces of $\frac{3}{4}$ in (19.0 mm) dia three strand nylon and was terminated with two 17 fm (31 m) pieces of $\frac{7}{8}$ in (22.2 mm) dia three strand nylon rope. All lines were cut into shorter lengths for easier stringing of floats.

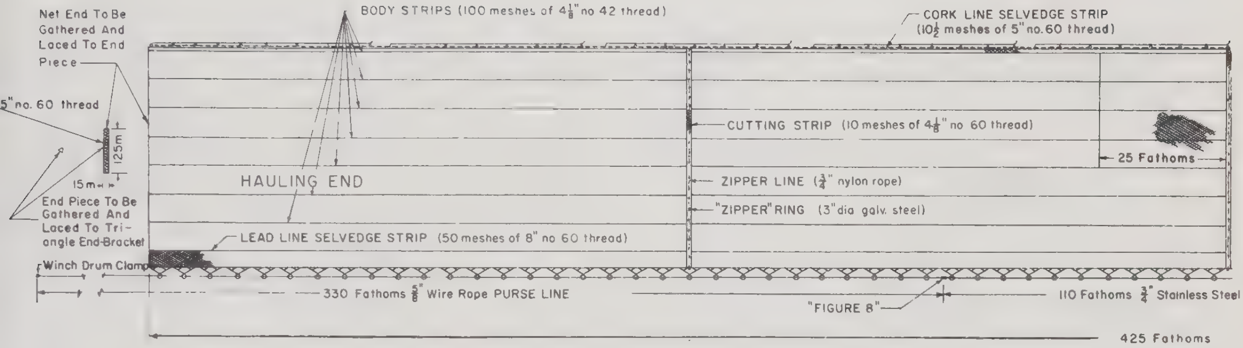

Net End To Be Gathered And Laced To End Piece
5" no. 60 thread
125m
15m
End Piece To Be Gathered And Laced To Triangle End-Bracket
Winch Drum Clamp
BODY STRIPS (100 meshes of 4 1/8" no 42 thread)
HAULING END
LEAD LINE SELVEDGE STRIP (50 meshes of 8" no 60 thread)
CORK LINE SELVEDGE STRIP (10 1/2 meshes of 5" no. 60 thread)
CUTTING STRIP (10 meshes of 4 1/8" no 60 thread)
25 Fathoms
ZIPPER LINE (3/4" nylon rope)
"ZIPPER" RING (3" dia galv. steel)
330 Fathoms 5/8" Wire Rope PURSE LINE
"FIGURE 8"
110 Fathoms 3/4" Stainless Steel
425 Fathoms

Fig 1. Standard U.S. tuna purse seine constructed of seven or eight strips each 100 meshes deep
M =

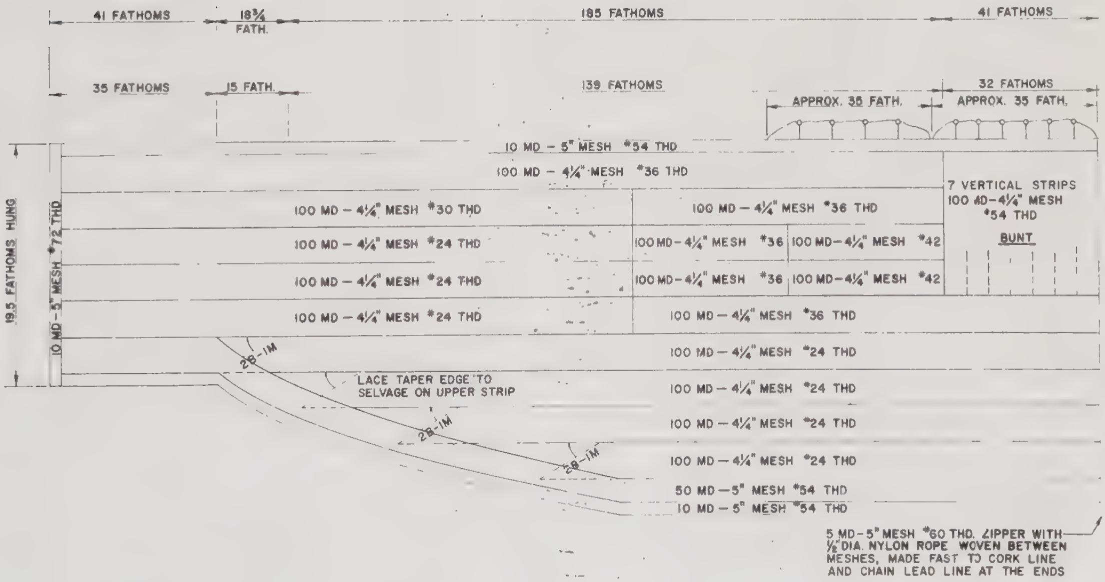
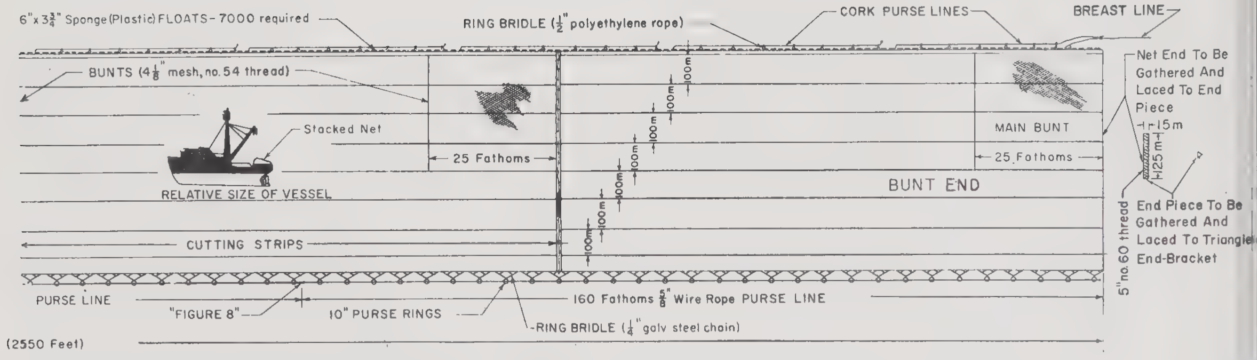
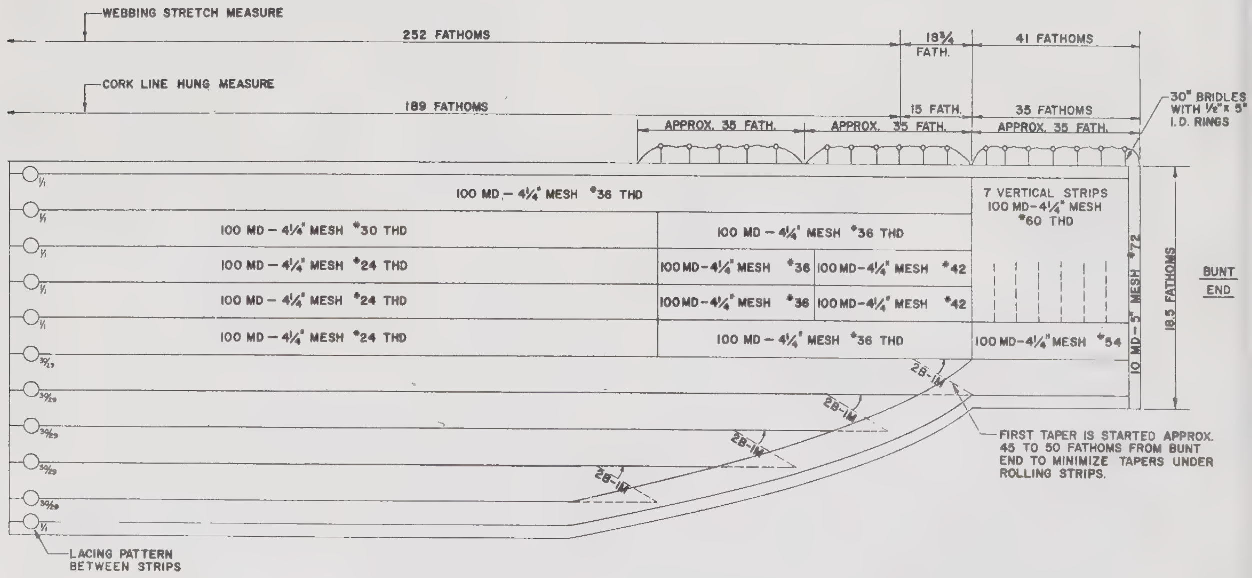

41 FATHOMS
18 3/4 FATH.
185 FATHOMS
41 FATHOMS
35 FATHOMS
15 FATH.
139 FATHOMS
32 FATHOMS
APPROX. 35 FATH.
APPROX. 35 FATH.
10 MD – 5" MESH #54 THD
100 MD – 4 1/4" MESH #36 THD
100 MD – 4 1/4" MESH #30 THD
100 MD – 4 1/4" MESH #36 THD
7 VERTICAL STRIPS 100 MD–4 1/4" MESH #54 THD
BUNT
100 MD – 4 1/4" MESH #24 THD
100 MD–4 1/4" MESH #36
100 MD–4 1/4" MESH #42
100 MD – 4 1/4" MESH #24 THD
100 MD–4 1/4" MESH #36
100 MD–4 1/4" MESH #42
100 MD – 4 1/4" MESH #24 THD
100 MD – 4 1/4" MESH #36 THD
BOAT END
19.5 FATHOMS HUNG
10 MD – 5" MESH #72 THD
100 MD – 4 1/4" MESH #24 THD
28-1M
LACE TAPER EDGE TO SELVAGE ON UPPER STRIP
100 MD – 4 1/4" MESH #24 THD
28-1M
100 MD – 4 1/4" MESH #24 THD
28-1M
100 MD – 4 1/4" MESH #24 THD
50 MD – 5" MESH #54 THD
10 MD – 5" MESH #54 THD
5 MD–5" MESH #60 THD. ZIPPER WITH 1/2" DIA. NYLON ROPE WOVEN BETWEEN MESHES, MADE FAST TO CORK LINE AND CHAIN LEAD LINE AT THE ENDS

Fig 2. Hybrid tuna purse seine
M = meshes; MD = meshes deep; FATH = fathoms;


6"x3¾" Sponge (Plastic) FLOATS - 7000 required
RING BRIDLE (½" polyethylene rope)
CORK PURSE LINES
BREAST LINE
BUNTS (4⅛" mesh, no. 54 thread)
Stacked Net
RELATIVE SIZE OF VESSEL
25 Fathoms
100 m
100 m
100 m
100 m
100 m
100 m
100 m
100 m
MAIN BUNT
25 Fathoms
BUNT END
Net End To Be Gathered And Laced To End Piece
15 m
125 m
End Piece To Be Gathered And Laced To Triangle End-Bracket
5" no. 60 thread
CUTTING STRIPS
PURSE LINE
"FIGURE 8"
10" PURSE RINGS
160 Fathoms ⅝" Wire Rope PURSE LINE
RING BRIDLE (¼" galv steel chain)
(2550 Feet)

which are laced in horizontally, and extend at full depth to the ends of the seine (McNeely 1961)
meshes


WEBBING STRETCH MEASURE
252 FATHOMS
18¾ FATH.
41 FATHOMS
CORK LINE HUNG MEASURE
189 FATHOMS
15 FATH.
35 FATHOMS
30" BRIDLES WITH ½" x 5" I.D. RINGS
APPROX. 35 FATH.
APPROX. 35 FATH.
APPROX. 35 FATH.
100 MD - 4¼" MESH #36 THD
7 VERTICAL STRIPS 100 MD - 4¼" MESH #60 THD
100 MD - 4¼" MESH #30 THD
100 MD - 4¼" MESH #36 THD
100 MD - 4¼" MESH #24 THD
100 MD - 4¼" MESH #36
100 MD - 4¼" MESH #42
100 MD - 4¼" MESH #24 THD
100 MD - 4¼" MESH #36
100 MD - 4¼" MESH #42
100 MD - 4¼" MESH #24 THD
100 MD - 4¼" MESH #36 THD
100 MD - 4¼" MESH #54
10 MD - 5" MESH #72
18.5 FATHOMS
BUNT END
1/1
1/1
1/1
1/1
1/1
30/29
30/29
30/29
30/29
30/29
1/1
2B-1M
2B-1M
2B-1M
2B-1M
FIRST TAPER IS STARTED APPROX. 45 TO 50 FATHOMS FROM BUNT END TO MINIMIZE TAPERS UNDER ROLLING STRIPS.
LACING PATTERN BETWEEN STRIPS

—netting and accessories.
THD = thread; B = bar; ID = inside diameter

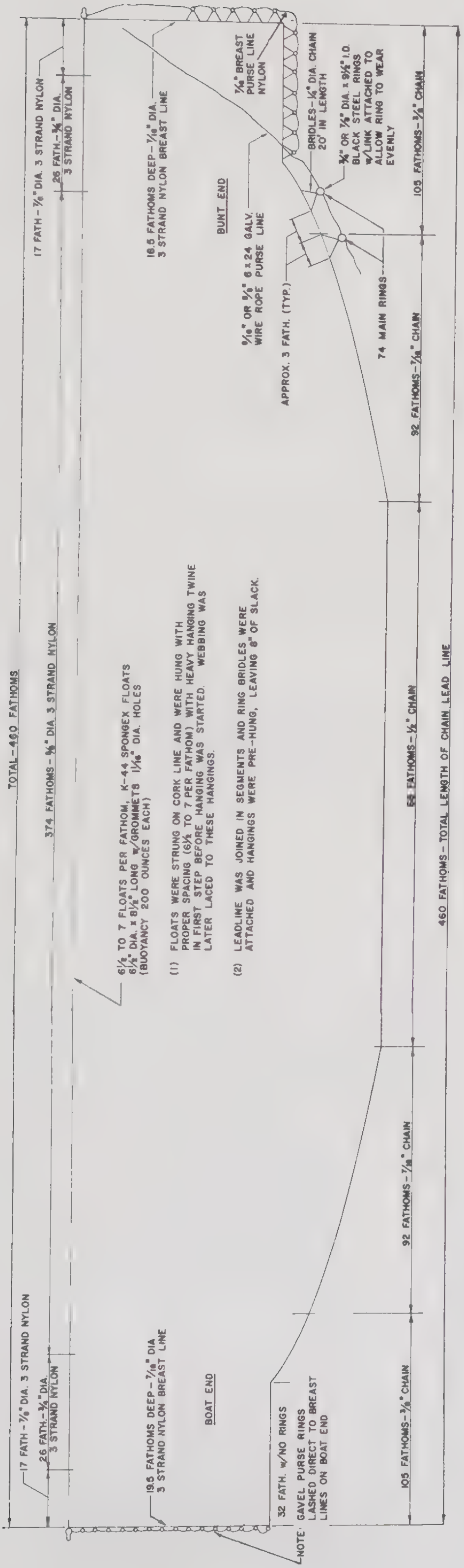

TOTAL-460 FATHOMS
374 FATHOMS-5/8" DIA. 3 STRAND NYLON
17 FATH-7/8" DIA. 3 STRAND NYLON
26 FATH-3/4" DIA. 3 STRAND NYLON
18.5 FATHOMS DEEP-7/16" DIA. 3 STRAND NYLON BREAST LINE
BUNT END
7/16" BREAST PURSE LINE NYLON
BRIDLES-1/4" DIA. CHAIN 20" IN LENGTH
3/4" OR 7/8" DIA. x 9 1/2" I.D. BLACK STEEL RINGS W/LINK ATTACHED TO ALLOW RING TO WEAR EVENLY
9/16" OR 5/8" 6x24 GALV. WIRE ROPE PURSE LINE
APPROX. 3 FATH. (TYP.)
74 MAIN RINGS
105 FATHOMS-3/8" CHAIN
92 FATHOMS-7/16" CHAIN
6 1/2 TO 7 FLOATS PER FATHOM, K-44 SPONGEX FLOATS 6 1/2" DIA. x 8 1/2" LONG W/GROMMETS 1 1/16" DIA. HOLES (BUOYANCY 200 OUNCES EACH)
(1) FLOATS WERE STRUNG ON CORK LINE AND WERE HUNG WITH PROPER SPACING (6 1/2 TO 7 PER FATHOM) WITH HEAVY HANGING TWINE IN FIRST STEP BEFORE HANGING WAS STARTED. WEBBING WAS LATER LACED TO THESE HANGINGS.
(2) LEADLINE WAS JOINED IN SEGMENTS AND RING BRIDLES WERE ATTACHED AND HANGINGS WERE PRE-HUNG, LEAVING 6" OF SLACK.
[illegible] FATHOMS-1/2" CHAIN
460 FATHOMS-TOTAL LENGTH OF CHAIN LEAD LINE
92 FATHOMS-7/16" CHAIN
17 FATH-7/8" DIA. 3 STRAND NYLON
26 FATH-3/4" DIA. 3 STRAND NYLON
19.5 FATHOMS DEEP-7/16" DIA 3 STRAND NYLON BREAST LINE
BOAT END
32 FATH. W/NO RINGS
NOTE: GAVEL PURSE RINGS LASHED DIRECT TO BREAST LINES ON BOAT END
105 FATHOMS-3/8" CHAIN

Fig 3. Hybrid tuna purse seine

U.S. tuna seines are usually hung with leadlines 5 to 10 per cent shorter than the corklines. This has been an accepted practice for tuna and salmon seines for many years. Salmon seiners in the Pacific Northwest and Alaska continue the 10 per cent shorter leadline practice because they feel it aids in the holding of salmon, when their seines are held open and towed with the power skiff and vessel. Although U.S. tuna seiners do not tow their seines, the 10 per cent shorter leadlines are possibly a leftover from these early ideas of seine fabrication.

Gavels and setback

The typical U.S. tuna seine has no gavels. The ends are baited to short border strips of netting 125 meshes long by 15 meshes deep, which in turn are laced to terminal stainless steel triangles. The full seven or eight strips are carried to the extreme ends of the seine, and the abrupt baiting of netting gives the appearance of gavels. However, this creates a large gap in the net wall under the vessel, leaving a possible escape route for encircled tuna. To help prevent this loss of fish, gavels or breastlines were installed at opposite ends of the hybrid seine. The bunt end was made 18½ fm (34 m) deep, and the back end was hung 19½ fm (36 m) deep. Small galvanized rings ½ in (12.7 mm) rod dia by 4 in (10.2 cm) inside dia (I.D.) were lashed to the upright breastline, made from $\frac{7}{16}$ in (11.1 mm) dia three strand nylon rope (fig 4). In order to distribute hauling strain on the netting more evenly, 32 meshes of the top of the gavel selvage strip are bunched and hung to the steel triangle or end piece (fig 5).

The hybrid seine was rigged without main purse rings or bridles for the first and last 35 fm (64 m). To fill this gap, a series of galvanized steel rings (½ in (12.7 mm) × 6 in (15.2 cm) I.D.) with nylon rope bridles were required. These rings were lashed under the end bunt with a ½ in (12.7 mm) dia nylon breast-purseline to purse the bunt end while the main purse rings are being drawn to the surface. This was done to permit the main wire purselines to work independently of the gavels, thereby permitting them to hang perpendicularly from the davit. An 18.5 fm (34 m) curtain of netting is thus formed directly under the boat.

On conventional U.S. tuna seines the ring bridles are connected the entire length of the chain leadline or with very little setback.

PHYSICAL PERFORMANCE

Based upon the performance of the scale Model II (Ben-Yami and Green, 1968), a prediction was made of the range of sinking performance of the hybrid purse seine at mid-net prior to start of pursing. This range was graphically compared to the measured sinking range of a conventional tuna purse seine (fig 6). The rather large depth range results from varying wind and current conditions affecting the sets.

A composite time-depth curve of the first five sets of the hybrid purse seine is also shown in fig 6. Agreement with the predicted range for a scaled-up Model II is considered good, allowing that the hybrid purse seine is deeper than the conventional seine by one strip of body netting.

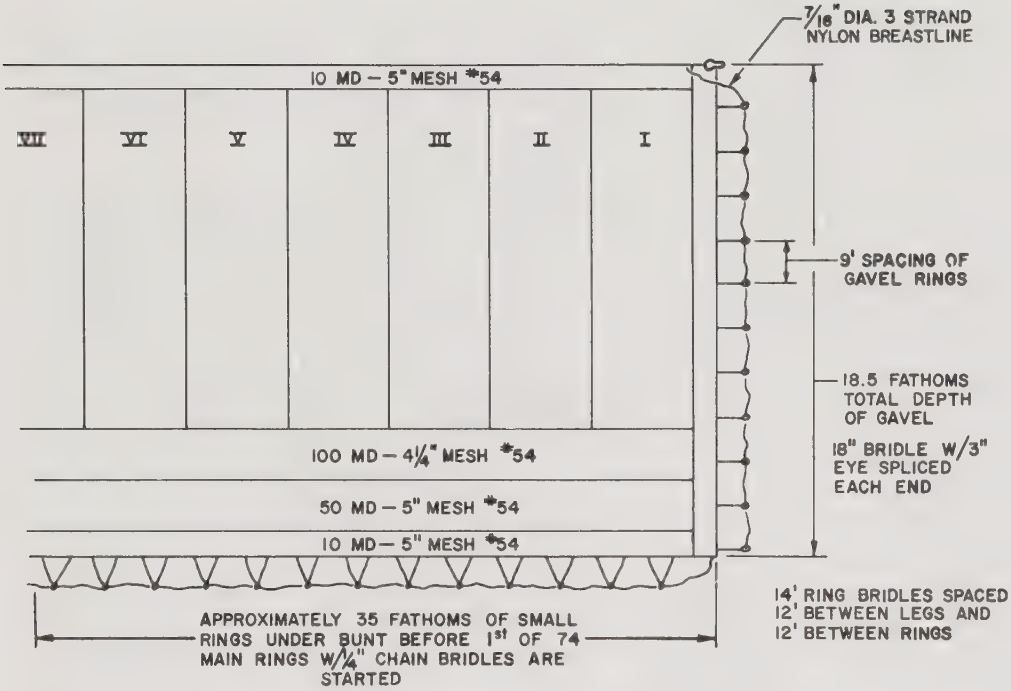

7/16" DIA. 3 STRAND NYLON BREASTLINE
10 MD – 5" MESH #54
VII
VI
V
IV
III
II
I
9' SPACING OF GAVEL RINGS
18.5 FATHOMS TOTAL DEPTH OF GAVEL
18" BRIDLE W/3" EYE SPLICED EACH END
100 MD – 4¼" MESH #54
50 MD – 5" MESH #54
10 MD – 5" MESH #54
14' RING BRIDLES SPACED 12' BETWEEN LEGS AND 12' BETWEEN RINGS
APPROXIMATELY 35 FATHOMS OF SMALL RINGS UNDER BUNT BEFORE 1st OF 74 MAIN RINGS W/¼" CHAIN BRIDLES ARE STARTED

Fig 4. Hybrid tuna purse seine—gavel or breastline and purse ring spacing

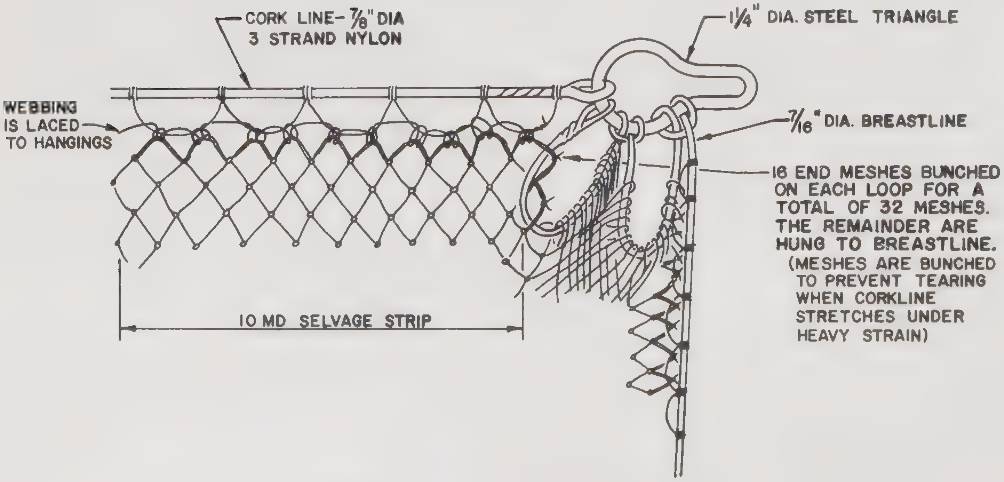

CORK LINE – 7/8" DIA 3 STRAND NYLON
1¼" DIA. STEEL TRIANGLE
WEBBING IS LACED TO HANGINGS
7/16" DIA. BREASTLINE
16 END MESHES BUNCHED ON EACH LOOP FOR A TOTAL OF 32 MESHES. THE REMAINDER ARE HUNG TO BREASTLINE. (MESHES ARE BUNCHED TO PREVENT TEARING WHEN CORKLINE STRETCHES UNDER HEAVY STRAIN)
10 MD SELVAGE STRIP

Fig 5. Hybrid tuna purse seine—bunt end detail

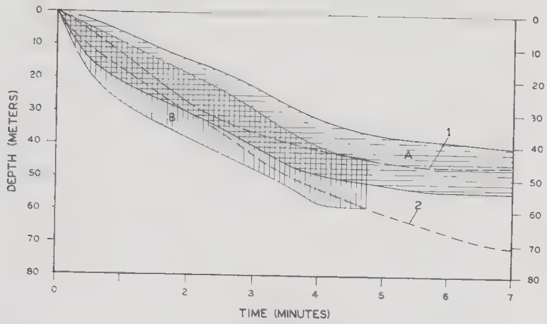


Fig 6. Predicted and actual sinking performance of hybrid purse seine. A = range of sinking performance of standard seven-strip tuna purse seine; B = predicted range of sinking performance of hybrid purse seine: 1 = mean sinking performance of standard seven-strip tuna purse seine; 2 = mean of first five sets of hybrid purse seine

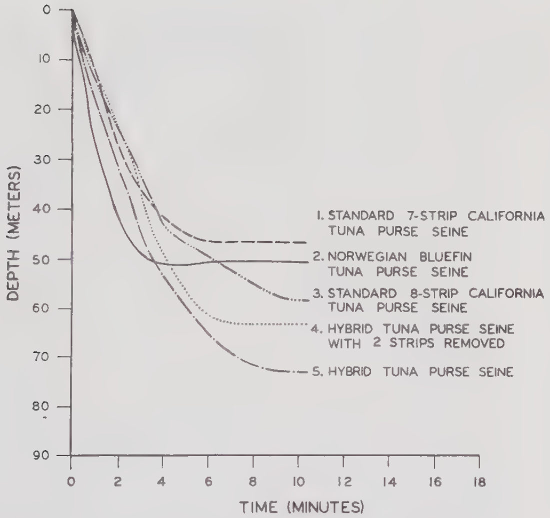


Fig 7. Midnet BKG traces from water entry to maximum depths. Source: 1—original BKG data. Means of nine sets of one net. 2—Hamre, 1963. 3—original BKG data. Means of nine sets of two nets. 4—original BKG data from one set of modified hybrid purse seine. 5—means of first five sets of hybrid purse seine

In fig 7 the sink rates and maximum depths of the Norwegian bluefin tuna purse seine and two California tuna purse seines are compared with those of the hybrid purse seine. While there is some crossing of lines, appearances indicate the initial sink rates generally are inversely related to the k_h of the nets, i.e. the two California purse seines, with $k_h = 0.91$, show the slowest sink rates, and the Norwegian purse seine, with $k_h = 0.40$, the fastest.

It is interesting to compare the hybrid purse seine modified to seven strips (see section 5) with the standard seven-strip California tuna purse seine. The former sinks approximately 9 fm (16.5 m) deeper, even though the numbers of body strips and therefore the stretched depth is the same in the two nets. The improved sinking performance results from the combination of (i) lower k_h, (ii) low ratio of corkline length to leadline length (gavels, in this respect, add to leadline length) and (iii) lighter netting.

Comparison of net ends

One objective of the hybrid purse seine design was to create a better underwater configuration at the net ends, reducing the gap under the boat, through which fish can escape and offering more efficient and economical use of netting. Figure 8 compares the wing ends of the hybrid purse seine and the standard seven-strip California purse seine at average maximum depth. In the section shown, the hybrid net is only four strips deep, whereas the standard purse seine is seven strips deep throughout its entire length. The hybrid purse seine's wing ends fish, on average, about 14 fm deeper with 1.7 times more filtering area using only about 0.62 the amount of body strip netting as the standard net. This improvement is due to three things: (i) the net ends laced to a long gavel line instead of gathering all of the webbing to a single point (the end triangle or swivel), (ii) the decreased k_h, and (iii) the setback of the first main purse rings to 35 fm (64 m) from the net end rings, allowing the gavels to hang free of the influence of the purseline.

Although pursing the gavels represents an extra task over the operation of the standard purse seine, they can be handled without loss of time. It was soon realized that only the front gavel, adjacent to the main bunt,

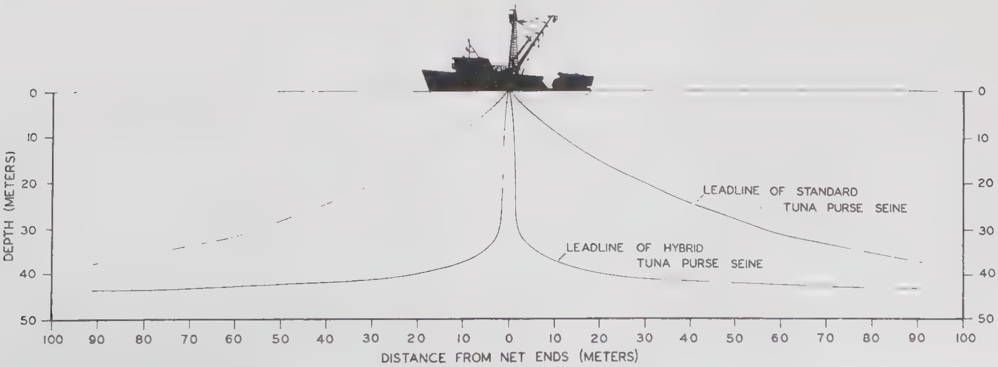


Fig 8. Net ends of hybrid purse seine and standard seven-strip tuna purse seine compared. Profiles shown are deduced from maximum depths of BKG traces. Tuna purse seiner shown to scale

needed to be pursed. There has been no tendency for the gavel to foul or roll up in the purseline.

The circle formed by the hybrid seine maintained its roundness and initial diameter well into the pursing stage. The floatline did not wrinkle up into folds, as is customary on conventional seines with 10 per cent shorter leadlines. The vessel has less tendency to pull itself into the centre with large pockets forming around the bow and stern, as happens with nearly all conventional tuna seine sets. With the hybrid seine, the roundness of the seine allows maximum holding area for the tuna that are encircled, keeping them alive longer. No measurements have been made of these phenomena, but all who have observed sets made by the hybrid purse seine agree in these subjective observations.

FISHING TESTS

The hybrid purse seine was placed on the purse seiner M/V *Liberty*, out of San Pedro, California, for fishing tests beginning August 1968. The previous rate of success of *Liberty* under its present crew (since 1 January 1968) was 56 per cent, not significantly different from that of other vessels fishing in the same area, which averaged 60 per cent. The net that *Liberty* had previously used was a standard U.S. tuna purse seine, seven strips deep by 350 fm (823 m) long with netting hung at a k_h of approximately 0.91.

During the remainder of 1968, after the close of the yellowfin season, *Liberty* made 19 sets with the new net: one on bonito, two on bluefin tuna, and 16 on albacore tuna. Seventeen sets were successful. The captain and crew were impressed with the net's sinking performance, the maintenance of the set's initial diameter well into pursing and, above all, its fish-catching ability. The only complaint was difficulty in stacking the net because of its incremental hang in. With more netting nearer the floats than the leadline, the net left the power block with a twisting motion with occasional large piles of netting falling down near the floatline. The power block had to be stopped often or slowed while the net was straightened out, and the net required 25 to 50 per cent longer than usual to stack.

During the first trip of *Liberty* in 1969, the hybrid seine was used under conditions for which it was not designed—on porpoise and in shallow waters. Because of the rough treatment received by the net when porpoise are involved, stouter than normal netting is usually used and a constant, not incremental k_h is needed for "backing down", a tactic of pulling the corkline underwater to allow porpoise to escape (Perrin, 1969).

Several sets on porpoise confirmed the belief that the hybrid purse seine, as hung, was not suitable for this type of fishing, because of a low rate of porpoise escapement and damage to the net by porpoise. After shipboard repairs were made, the seine was used around the Revillagigedo Islands off Mexico, a place well known for rough, shoaling bottoms (and often plentiful tuna). The ill-fated trip ended with half a load of fish when the net snagged bottom, and over half the leadline was lost. Seven of 13 sets were successful.

In anticipation of further porpoise fishing during the yellowfin tuna season, we temporarily modified the seine by increasing the k_h to 0.83 and removing two strips. The incremental hang-in was abandoned. We replaced 250 fm (457 m) of lost leadline in the back portion of the net with $\frac{7}{16}$ in (11.1 mm) dia chain.

During the following three trips, March to June 1969, there was no opportunity to test the net, in its modified form, on porpoise. On schoolfish—bluefin, skipjack, and yellowfin tuna, and a small amount of bonito—however, it performed well. Of 52 sets, 33 (63 per cent) were successful. Schools as large as 100 short T (91 metric T) were landed, using only the main bunt, thus proving the adequacy of the light-weight netting for handling heavy loads of fish. The sink rate and depth of the hybrid purse seine, although it had been reduced to seven strips, greatly exceeded that of the standard seven-strip purse seine (fig 7).

In June 1969, after the close of the yellowfin tuna season, the hybrid seine was restored to its original configuration with the exception of the incremental hang-in. With incremental hang-in, the mean k_h of all the strips at mid-net was 0.79. We rehung the seine at this new k_h, lacing all the strips together evenly. The leadline, with the chain replacement made in the previous modification, remained the same. We then checked the net's sinking performance with BKG's and found the curves to be nearly identical to those obtained with its original configuration.

Two more trips were made with the hybrid purse seine before *Liberty* ceased fishing for the year. During those trips, a total of 37 sets were made, of which 18 (49 per cent) were successful.

Fishing test results

We compared the rates of success of *Liberty* and other vessels for the period during which *Liberty* was operated under its present ownership and crew (since 1 January 1968). Fishermen's logbook data were made available to us for this purpose by the Inter-American Tropical Tuna Commission (IATTC). Because the rate of success may vary with time, area, vessel size, and type of fishing (e.g. species and "porpoise" fish versus schoolfish—Craig Orange, IATTC, personal communication), data were used only from those vessels most comparable to *Liberty* in these respects. This was accomplished by simply tabulating sets made north of 20°N latitude and in the Revillagigedo Islands—Hurricane Bank area. This northern area of the fishery nearly approximates the traditional fishing grounds of small- to medium-size purse seiners like *Liberty*, whose main strategy is to concentrate on yellowfin, skipjack and bluefin tunas as these fish appear seasonally. The porpoise fishery is centred in southern, more tropical waters (Perrin, 1969). Moreover, at any given time the majority of the small purse seiner fleet may usually be found concentrated in a smaller area within the northern region just defined, as they move with the fish. The few sets made on porpoise were omitted from these data, except during one quarter when *Liberty* made sets on porpoise. For two quarters when *Liberty* fished farther south, we tabulated data from other vessels fishing in the same 5° squares.

The purse seines carried by the other vessels are all versions of the standard U.S. tuna purse seine described by McNeely (1961) with only minor variations in design and size.

In order to examine our set data by time, we tabulated them by trips in the same manner as the IATTC compiles data obtained from fishermen's logbooks—by quarters of year in which the trips originated. The results in success ratio by quarters of years are shown in fig 9. *Liberty's* success ratio, which commenced below that of comparable vessels, surpassed them in the quarter in which she started using the hybrid purse seine and maintained these higher levels during the remainder of the test period.

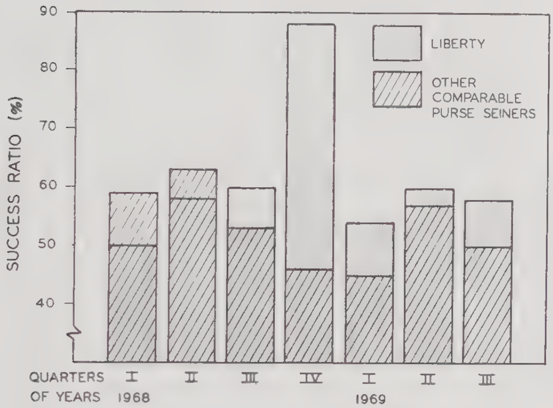


Fig 9. Success ratios of Liberty *compared to similar purse seiners by quarters of years. Hybrid purse seine added to* Liberty *during third quarter of 1968*

For statistical comparisons, all of the set data are summarized in Table 2.

TABLE 2. SET DATA OF *Liberty* COMPARED WITH OTHER COMPARABLE PURSE SEINERS BEFORE AND DURING THE USE OF THE HYBRID PURSE SEINE BY *Liberty*

	Before use of hybrid purse seine by Liberty		*During use of hybrid purse seine by* Liberty	
	Number of sets	*Per cent success*	*Number of sets*	*Per cent success*
Liberty				
Successful sets	44		75	
Unsuccessful sets	35	56	46	62
Total sets	79		121	
Other comparable purse seiners				
Successful sets	2,067		1,525	
Unsuccessful sets	1,473	58	1,416	52
Total sets	3,540		2,941	

All adjacent pairs around the perimeter of the table were tested for significant differences at the 0.05 level using chi-square in 2×2 contingency tables. The only significant difference was between other comparable purse seiners and *Liberty* during her use of the hybrid purse seine.

DISCUSSION AND CONCLUSIONS

Some shortcomings in the fishing test data hampered their accurate interpretation. Among these are the modifications of the hybrid purse seine during the test period, and the variability encountered in fishing conditions and species fished. Our testing vessel was an unpaid volunteer and had to continue normal operations without outside interference in this highly competitive fishery; therefore this phase of the experiment could not be carefully controlled.

Our interpretation of the data is that because there were no differences between the success of the *Liberty* and success of the other boats before the new net was used and because no other variable has been introduced or cause of variation detected, we may ascribe any difference after the new net was adopted as being associated with the *Liberty's* use of the hybrid purse seine.

Difficulty was also encountered in precisely interpreting the sinking data of purse seines because of lack of control over natural conditions affecting the set and because of the absence of basic studies that define relationships between net performance and setting conditions. For example, the effect of wind and current driving boat and net apart is to limit the seine's maximum depth. This relationship has often been observed but never defined quantitatively. Indeed, the presence of a current may often go undetected. It could probably be shown that pursing speed and mesh and twine sizes, among other factors, also influence the wind and current's effect on the seine's sinking. Until such basic research on purse seine performance has been conducted, it is necessary to use averages of repeated measurements.

The ability to make high speed sets is of great importance to eastern tropical Pacific tuna purse seiners which make sets at speeds of 7 to 8 kn, and sometimes faster. This leads us to believe that tuna seines should be hung at k_h of no less than 0.7, preferably between 0.75 and 0.80. Although limitation of k_h does not permit maximum depth per given strip, it does preclude tearing of netting when high speed sets are necessary. Seines can always be made deeper by adding additional strips. Besides, any deviation to one side or the other of the square meshes obtained with $k_h = 0.7$ results in decreasing economic efficiency of use of netting. With $k_h > 0.7$, square meshes will be achieved at some point during sinking or pursing of the seine; but at $k_h > 0.7$, this is never possible.

The effects of the main features of the hybrid purse seine which differentiate it from standard U.S. tuna seines may be summarized as follows:

1. Lighter netting—gives easier handling, large net size for given size of net pile, and faster sinking.
2. Lower k_h—contributes to greater sink rates and fishing depths, uses netting more economically, contributes to more open net circle for a longer time during set but may cause some difficulty for porpoise escapement.
3. Tapering—maintains depth where needed, eliminates unnecessary netting at ends, and aids in drying-up fish prior to brailing.
4. Incremental hang-in—might offer better pur-

sing configuration but contributes to handling difficulty and low porpoise escapement.

5. Floatline and leadline of equal lengths—contributes to greater sink rates and fishing depth and more open net circle longer during set.

6. Gavels with breast pursinglines—uses netting at net ends more economically, reduces escape gap under the purse seiner and adds to the effective length of the leadline.

7. Setback of main purse rings from net ends—contributes to vertical hanging of gavels beneath vessel, reducing this escape gap.

Acknowledgments

The authors deeply appreciate the cooperation of the owners, captain and crew of *Liberty* who so generously provided their ship time, space, personal cooperation, and hospitality during the testing of the hybrid purse seine.

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7108

The American Tuna Purse Seine Fishery

La pêche américaine du thon à la seine coulissante

La pêche américaine du thon à la seine coulissante a lieu sur l'albacore (*Thunnus albacares*), le listao (*Katsuwonus pelamis*), le thon reouge (*Thunnus thynnus*) et le germon (*Thunnus alalunga*). Cette pêche, qui débuta peu après 1900, s'est développée dans trois directions: pêche à l'appât vivant pour l'ensemble des quatre espèces; pêche à la seine coulissante pour le thon rouge, le listao et l'albacore; pêche aux lignes traînantes pour le germon. La pêche à l'appât vivant a été la plus importante jusque vers 1960. Par suite de la contrainte économique et des progrès technologiques qui ont amélioré l'efficacité de la seine coulissante, presque tous les thoniers clippers à l'appât vivant ont été transformés en seineurs durant la période 1957–61. La période 1961–70 a été caractérisée par le développement et la modernisation de la flottille des seineurs. Actuellement, plus de la moitié du tonnage et environ un tiers de cette flottille sont constitués par de grands navires récents, construits pendant cette période. Avec l'avènement d'une réglementation par quota concernant l'albacore dans le Pacifique tropical oriental et la durée de plus en plus courte chaque année des saisons ouvertes à la pêche, les grands seineurs ont commencé à étendre leurs opérations dans des secteurs en dehors des lieux de pêche américains traditionnels du Pacifique oriental. Ces bateaux sont de plus en plus nombreux à se déplacer vers l'ouest, à l'extérieur de la zone réglementée, et vers l'est, en Atlantique, jusqu'à la côte d'Afrique. La production du thon a commencé à diminuer en Californie méridionale, car la plupart des nouveaux seineurs ont choisi Puerto Rico comme port d'attache. On s'attend à l'avenir à voir un accroissement de la demande et des prix du thon avec des captures en augmentation, une exploitation de nouveaux secteurs et des rendements de pêche en diminution. Si les Etats-Unis veulent rester compétitifs, de nouveaux progrés devront intervenir dans la echnologie de la pêche du thon à la seine.

La pesquería norteamericana del atún con redes de cerco de jareta

La pesquería norteamericana del atún con redes de cerco de jareta se dedica al rabil (*Thunnus albacares*), barrilete (*Katsuwonus pelamis*), atún de aleta azul (*Thunnus thynnus*) y albacora (*Thunnus alalunga*). La pequería del atún comenzó poco después de 1900 y se desarrolló en tres direcciones: pesca con cebo vivo de las cuatro especies; pesca con artes de cerco de jareta del atún de aleta azul, el barrileta y el rabil; y pesca con curricán de la albacora. Hasta 1960 la más importante fue la pesca con cebo vivo. A causa de la presión económica y de los progresos tecnológicos que incrementaron la eficacia de la pesca con artes de cerco, casi todos los clíperes destinados a la pesca del atún con cebo vivo se transformaron en cerqueros en el período 1957–61. El período 1961–70 se caracterizó por el aumento y modernización de la flota de cerqueros. En la actualidad, más de la mitad del tonelaje y cerca de un tercio de la flota de barcos cerqueros está constituído por embarcaciones grandes y nuevas, construídas durante dicho período. Con la implantación de un sistema de cupos para la pesca del rabil en el Pacífico oriental tropical y con la consiguiente reducción progresiva de la temporada anual de pesca, los grandes cerqueros han empezado a extender sus operaciones a zonas situadas fuera de los caladeros americanos tradicionales del Pacífico oriental. Son cada día más las embarcaciones que se dirigen hacia el oeste, saliendo de la zona regulada, y hacia el este, penetrando en el Atlántico en dirección de la costa africana. La producción de atún ha empezado a desplazarse del sur de California, porque la mayor de los nuevos cerqueros han escogido Puerto Rico como puerto base. En el futuro, es de esperar un aumento de la demanda y de los precios del atún, a la par que un aumento de las capturas y la explotación de nuevas zonas, con una disminución de los índices de captura. Si los Estados Unidos quieren mantener una posición competitiva, será preciso que se introdurcan nuevos adelantos en la tecnología de la pesca del atún con artes de cerco de jareta.

THE American tuna fishery depends mainly on four species: yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) found mostly in the tropics and constituting the bulk of American tuna landings; and bluefin (*Thunnus thynnus*) and albacore (*Thunnus alalunga*) in temperate regions. In 1960 to 1968, the annual U.S. tuna catch was about 145,000 to 193,000 t (Lyles, 1969). Principal fishing methods are purse seining, pole and line fishing with live bait and trolling.

The present American tuna purse seine fleet stands out as one of the most modern and efficient in the world. The purse seiners are among the largest, most complex and costly of fishing vessels. The growth of this fishery in a country where fishing has, for many years, declined in relative national and world importance seems almost a paradox. The fishery is marked by alternate crises and massive responses to them.

Knowledge of the origins of tuna purse seining is basic to understanding currently used gear methods. Purse seining for tuna began out of San Pedro, California, about 1914. The first purse seines used were designed primarily for "whitefish" (barracuda, white seabass and yellowtail). A typical "whitefish" net was 200 fm long and 18 fm deep. The stretched mesh size was $2\frac{1}{2}$ in., constructed of No. 12 (827 Tex) cotton twine. The netting was hung tightly to the floatline with hanging coefficients (k_h) of 0.91–1.0 (hanging coefficient (k_h): ratio of length of line to adjacent stretched length of webbing (Ben Yami, 1959)). The rope leadline was 10 to 15 per cent shorter than the floatline. The wing ends terminated at vertical breastlines which were usually about half of the net's depth. This net was adapted from the salmon purse seine design used in the Pacific Northwest. Aside from material and size, these early "whitefish" nets are remarkably similar in basic design to tuna purse seines in use today. Typical purse seiners then were about 50 ft long with 12 ft beam.

The first purse seine designed specifically for tuna was built about 1916 by Van Camp Sea Food Company. This net was 420 fm long by about 35 fm deep. The stretched mesh size was 11.4 cm constructed mainly of No. 36 cotton. A surplus navy tow boat, 33.4 m long was converted to a purse seiner to handle this net. This first experiment with a "big boat" and "big net" was doomed to an early failure. The bulky net proved too unwieldy to manage. In less than a year this experiment ended and two smaller purse seines were made from this net and fished from the *A.M.Z.* and *California*, both purse seiners of about 15.2 m length.

During the first summer with this cut-down tuna purse seine, the *A.M.Z.*, under Captain Anton Zankich, set on a large school of bluefin. All but 10 to 15 t was lost because of handling difficulties. This gave rise to optimism that net handling methods could be improved so that tuna schools much larger than five or six t could be taken for canning. Commencement of bluefin canning about 1918 was probably the salvation of the industry. The increased market attracted more salmon seiners from the State of

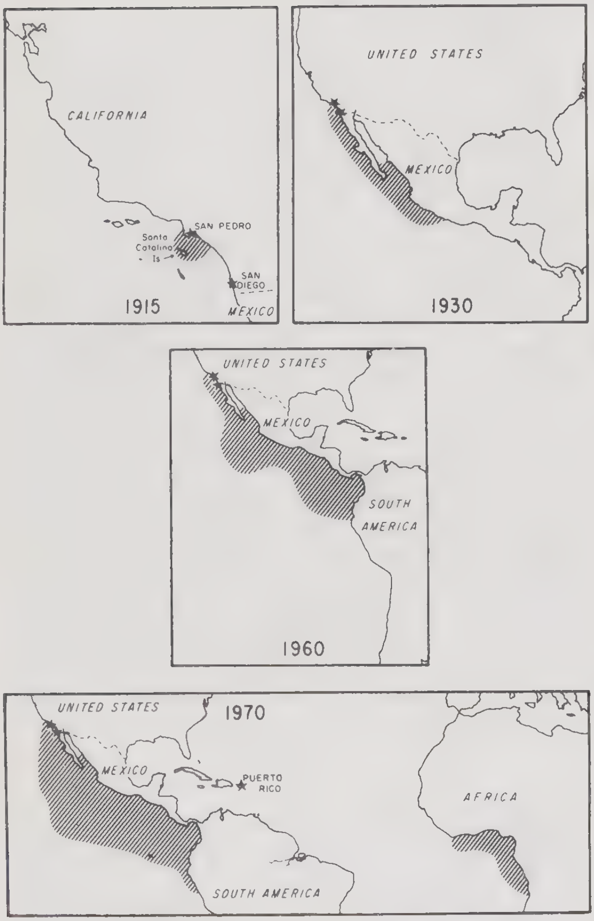

*Fig 1. Expansion of U.S. tuna fishing areas, 1915–1969. * = tuna purse seining ports*

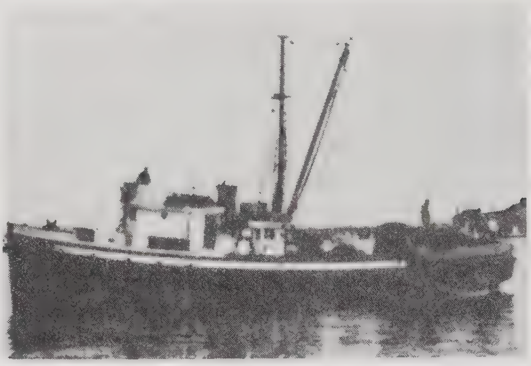

Fig 2. Tuna purse seiner Oakland. *82 ft long with 21½ ft beam. Photo by R. S. Croaker, Calif. Dept. of Fish and Game, Jan. 1931*

Washington until a peak of about 125 purse seiners was attained in the San Pedro bluefin fleet. Because of technological difficulties, however, the success of this large fleet was poor and by 1920 most of them had returned to their original ports.

In 1923 the *Diamond*, under Pete De Maria, was the first tuna purse seiner to fish Mexican waters as far south as Cape San Lucas (*Diamond* also had the first diesel main engine in the fleet, a 100 hp Fairbanks Morse). By 1929, led by the *Sea Rider*, built by Captain Peter Dragich, Sr., purse seiners as large as 100 t capacity were being built specifically for operating off Baja California and had begun to take tuna from the Gulf of California.

Power brailing and the boom and winch to haul the net had been developed by this time. The net was strapped and pulled in, a section at a time, with the winch and block from the main boom. The same type of gear was also being used to mechanize the "drying up" operation. A technique for "cutting" the net to divide large catches into more manageable portions was also developed.

With the development of mechanized methods of net handling, the purse seines were made larger—up to 300 fm long by 28 fm deep—and of heavier construction. Through more trial-and-error experimentation, optimum mesh size stabilized at 10.8 to 11.4 cm stretched mesh. The main drawback of these nets was still the cotton material. Rapid deterioration started from first use and netting two years old, if it lasted that long, was worthless. Nets were constantly being repaired. Whenever there were spare moments, men were replacing panels, shifting rotten netting to areas of lesser strain and sewing holes and rips in badly decayed cotton.

The use of ammonia refrigeration, in conjunction with crushed ice, began in 1930, when purse seiners *Musketeer* and *White Star* installed refrigeration coils in the fish holds to extend the usefulness of ice. The use of refrigerated brine followed in 1932—preceded by its successful use on a bait-boat. At first the brine was circulated through a cooler and then through the fish wells which did not contain cooling coils. Slowly, vessels of the purse seine fleet began to add, or were built with, refrigeration machinery and by 1945 all these seiners were so equipped.

The purse seiner fleet generally operated locally from the Channel Islands off San Pedro south to the waters along both sides of Baja California. Some of the larger vessels, however, did venture farther south. In 1932, Captain Nick Dragich took the *Sea Tern* (previously named the *Musketeer*), a 32 m purse seiner of 136 t capacity, to the Galapagos Islands. Dragich was also the first to set on porpoise schools for the tuna found with them. A purse seiner of this time period is shown in fig 2. After the late 1930's, the normal maximum run for San Pedro tuna purse seiners was to between Manzanillo and Acapulco, Mexico.

Starting in the period 1925–28, purse seines were adopted for sardine fishing at San Pedro and began to replace the lampara nets previously used. For the next 20–30 years, until the decline in abundance of the California sardine and mackerel resources, purse seining for tuna was of secondary importance for many of these smaller purse seiners. They fished for tunas when they appeared during the off-season for sardines (Shimada and Schaefer, 1956).

With improved refrigeration making longer trips possible, further increased vessel size appeared to be logical. In 1937, the first steel hulled purse seiner, *Paramount*, was built. This vessel was 37½ m long with a capacity of 309 t. It carried a net 420 fm long by 42 fm deep. In 1947, the *Santa Helena*, capable of loading 328 t of tuna, was built. Her net was 500 fm long by 45 fm deep—but still of cotton. The practice of tarring nets to help extend their life had long been practised by this time, but the tar added significantly to weight. With the corks then used, the *Santa Helena's* giant net would not stay afloat during pursing, but the problem was solved by lashing about twenty oil drums along the corkline.

The trend to larger purse seiners culminated in the *Falcon*, a converted 53.5 m Navy tow boat capable of carrying about 600 t of tuna. She had the shortest career of the fishing fleet. Her maiden voyage lengthened into weeks, then months as her weary crew bent to the discouraging task of filling her insatiable holds. Finally, she returned to port with about a half load and retired from fishing.

It was found that some of these larger purse seiners could operate more profitably as bait-boats, and several were converted. Paralleling the early growth of the tuna purse seine fishery, the bait-boat fleet at San Diego developed in size and numbers and began to extend operations as far as Peru. Thus, while one segment of the U.S. tuna fleet developed an efficient purse seine technology, but remained largely on local fishing grounds, the other segment, with their large and modern tuna clippers, developed familiarity with distant grounds. By the late 1950's, all the ingredients for a successful high seas tuna purse seiner fleet were present in these two fleets. The catalyst that brought them together was a growing economic crisis for American tuna fishermen.

THE TRANSITION PERIOD

Purse seining in the tropics was carried out by American fishermen from 1925 on, but with limited success because of rapid deterioration of cotton netting. In the 1950's, an economic squeeze caused by low-priced imports of Japanese-caught tuna, forced American fishermen to increase their efficiency, and they concentrated on purse seining technology. This time, due to two major technological developments, nylon nets and the power block, the method became feasible for fishing with very large nets in warm waters. The first all-nylon tuna seine, however, was not an American innovation as popularly thought (and as stated by McNeely, 1961), but was fished by a Peruvian boat in 1954 (Anon, 1959). The first American use of an all-nylon seine for tuna was in 1956 by the *Anthony M*. (Anon., 1956.)

The now well-known advantages of synthetic fibre nets in giving superior strength and larger catches were followed by the puretic power block. This was introduced to tuna seining by *Anthony M* in 1955. The largest contribution of the power block was in time saved in retrieving the net after an unsuccessful set. The time was reduced by nearly half (Orange and Broadhead, 1959), thus allowing many more sets of a large net to be made in one day.

Spurred by the success of the *Anthony M* with the new gear, the Peru-based American clipper *Sun King* in 1957 was converted to purse seining, and the first American-based clipper to be converted, the *Southern Pacific*, became a seiner soon after. A chain reaction followed, and by 1961 about 75 vessels were converted or undergoing conversion.

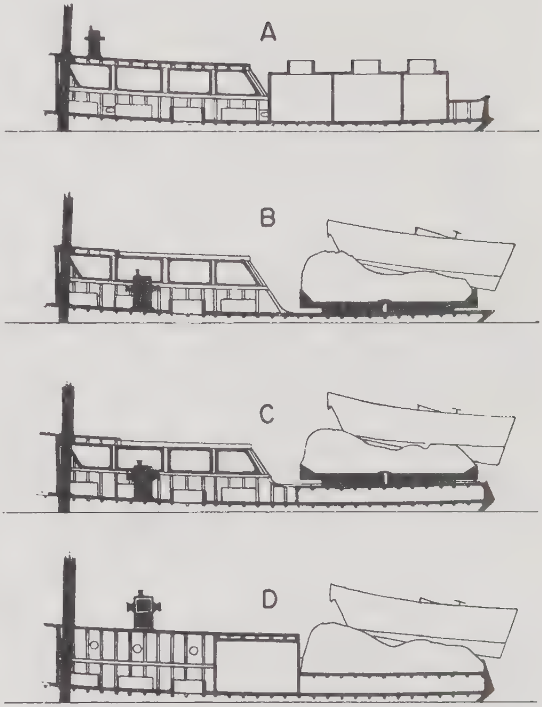

Fig 3. Stern cross sections showing: A, typical tuna clipper; B, turntable, net and skiff on early conversion; C, watertight void space under turntable improves vessel safety; D, enclosed lower deck, raised net platform, and deck-mounted fish well increases fish-carrying capacity. (After McNeely, 1961)

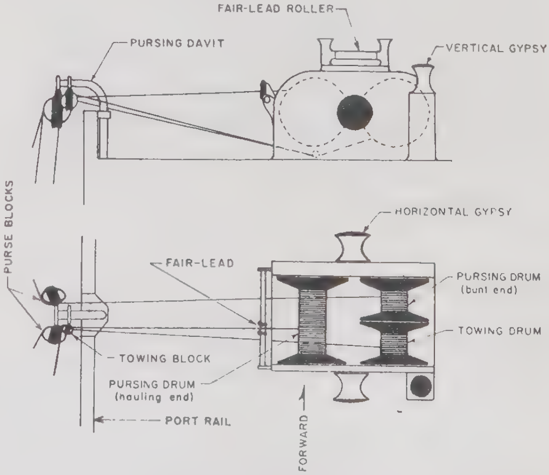

Fig 4. Purse seine winch drum and cable arrangement (After McNeely, 1961)

Table 1 shows that in 1961 the number of seiners in the long-range fleet was more than twice that in 1958. Today, there are very few bait-boats left (43 out of a fleet of 163 vessels), and the tuna fishery is effectively a purse seine fishery.

TABLE 1. LONG-RANGE CALIFORNIA AND PUERTO RICO BASED VESSELS ENGAGED IN THE EASTERN TROPICAL PACIFIC TUNA FISHERY DURING THE YEARS 1950–1969

Year	*Baitboats*	*Purse seiners*	*Total*
1950	204	67	271
1955	172	63	235
1959	140	53	193
1960	70	83	160
1961	44	114	158*
1962	36	103	139
1965	44	111	155
1968	50	104	154
1069	43	114	157

* Does not include about 22 other (mostly under United States flag) based in Costa Rica, Mexico and Peru.

Source: Inter-American Tropical Tuna Commission, as reported in McNeely (1961) and Annual Reports of the Inter-American Tropical Tuna Commission for 1967 and 1969.

Cost of earlier conversions varied between US$50,000 and US$100,000 depending on design and quality of materials and workmanship. Added was the cost of a nylon purse seine averaging about US$50,000.

Fig 5. Vivian Anne *entered the fishery in 1969. Length 144 ft, capacity 465 tons. Photo courtesy of Arthur DeFever, Naval Architect*

Details of conversion

The earliest conversions from clipper to seiner involved little more than clearing away the gear and structures required for bait fishing and installing those for seining. The bait tanks, piping, circulation pumps, fishing racks and accessory gear were removed, leaving a clear afterdeck for the seine-fishing gear. Amidship upper decks were partially cut away on the port side aft.

An auxiliary speedboat and accessory gear were stored on remaining upper deck space aft, and guard rails were installed around exposed sections of upper decks. No hull modifications were required.

It was necessary to install masts and booms to withstand the stresses of net hauling, "drying up" and lifting aboard the heavy seine skiff. These were constructed of double strength tubular steel with multiple diameters fitted one inside the other and welded at external joints.

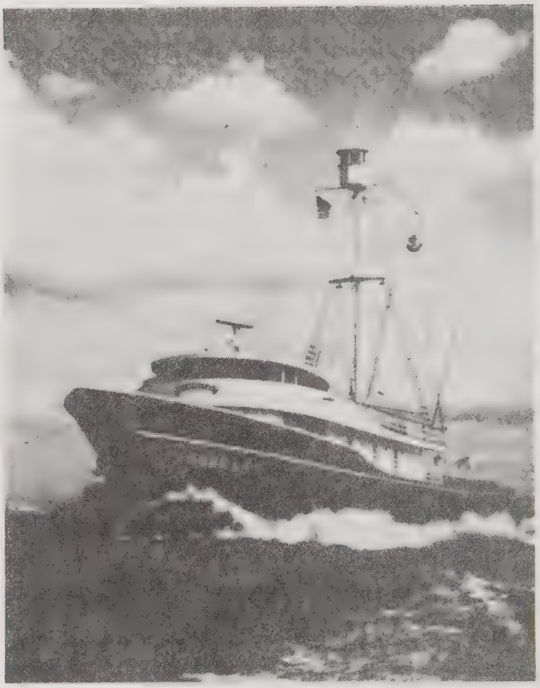

Fig 6. Cabrillo *entered the fishery in 1968. Photo courtesy of J. M. Martinac Shipbuilding Corp.*

Seining operations also require a heavy-duty winch. The winch used in early conversions had a minimum of three drums, two gypsies and two heavy-duty lashing bits (fig 4, from McNeely, 1961). The following description of the winch is repeated verbatim from McNeely (1961):

> "Drums—Three drums are mounted on two parallel drivershafts running fore and aft in the winch housing (fig 4). The single purseline drum located on the port driveshaft holds about 600 fm of wire rope purseline made of two end sections measuring 160 fm and 330 fm long . . . $\frac{5}{8}$ in (1.6 cm) diameter galvanized steel and a 110 fm centre section made of $\frac{3}{4}$ in (1.9 cm) stainless steel wire rope. Two drums, located on the starboard driveshaft, have independent drives and controls. The forward

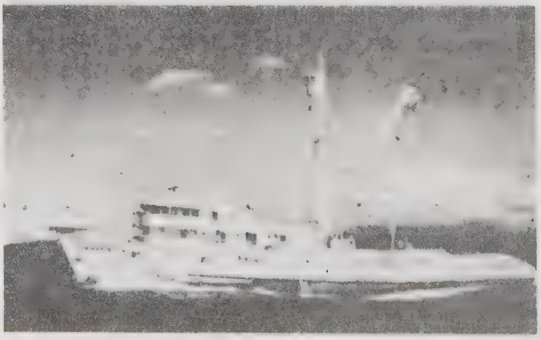

Fig 7. Marietta *entered the fishery in 1968. Photo courtesy of J. M. Martinac Shipbuilding Corp.*

> drum in the double drum section is used to haul in the bunt-end purseline, while the after drum is used to hold approximately 200 fm of ⅝ in (1.6 cm) galvanized steel wire rope towing cable. Roller fairleads on the base or on top of the winch guide cables from the starboard drums past the port drum and through a purse block and towing block mounted on the purse davit by the port rail. Level-wind fairleads are driven manually or by hydraulic or air motors and usually are installed on the port drum only. Clutches and brake shoes on the pursing drums and towing drum are operated manually or by hydraulic or air cylinders. One newly designed winch has small control levers, mounted in a control console . . . to allow operation of all drums simultaneously by one winch operator.
>
> "Cargo drum—A fourth drum (cargo drum) of small diameter is sometimes located above and between the two large drum sections. It is used principally for operation of a "choker" rope during "sacking-up" operations. Fairlead blocks on the starboard rail lead the choker rope along the starboard rail aft and then to the port rail where strapping and choking operations are performed.

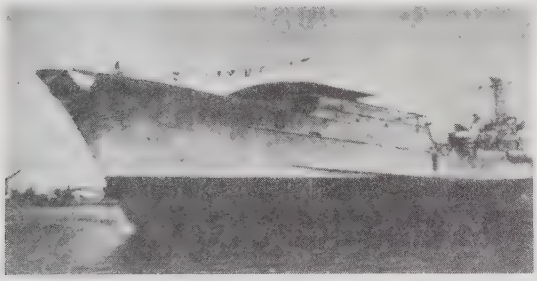

Fig 8. Hull 79 under construction. Length 200 ft, capacity 1,335 tons. Photo courtesy of Campbell Machine, Inc.

> "Gypsies—Two 12 in (30.4 cm) horizontal gypsies, and sometimes an additional 10 in (25.4 cm) vertical gypsy, are mounted on the winch for general utility hauling. The forward horizontal gypsy is used more frequently than the other two and has sea water piped to it for cooling purposes during long periods of holding . . . Nylon, manila and wire ropes are commonly hauled on the seine-winch gypsies. When hauling of wire rope is anticipated, surfaces of gypsies are hardened.
>
> "Power supply—A variety of power supplies are utilized to operate seine winches. One of the more common drives is the electric motor which, due to the small space available in the shaft alley beneath the winch, is applicable as well as economical. Some vessels employ hydraulic motors or diesel engine drives coupled through line shafting or mounted directly beneath the winch. The vulnerability of electric motors and controls to damage from salt water, and the advantage of controllable speed and torque in hydraulic drives, makes installation of the latter power source desirable."

Use of a power block required a hydraulic drive, and complete hydraulic drive systems for boom-topping winches, vanging winches and the pursing winch were soon adopted by the fleet.

Special fore-deck installations are required for operation of a purse seine, including rail cleats, rope fairlead sheaves and cork purseline winches. The corkline is pursed by passing lines through a port rail sheave to the corkline winch or to the anchor winch gypsy.

A special heavy-duty davit at the port rail in line with the pursing winch supports the purse blocks and the towing block. The davit is constructed by bending a heavy steel pipe to form a right angle elbow and welding a steel plate stiffener across the angle for support. Heavy duty purse blocks are mounted fore and aft on hanger eyes constructed of heavy steel plate and welded to the pipe on the outboard end, and a smaller towing block is attached to a third eye on the upper side of the davit.

The turntables, which were included in the early conversions, were about 7.6 m square and constructed of heavy timbers. Support was provided by heavy-duty steel roller pedestals secured to the deck, and the table rotated on a circular steel track attached to its underside.

Fish hoppers to receive brailed fish were constructed in a variety of shapes and materials. The hopper was positioned and pivoted in a socket installed on the deck. A chute from the hopper to the wells was constructed in sections, of sheet metal and Y-shaped pedestals supported it along the deck.

The seine skiff

The size of the seine skiff is directly related to the size of the net and the size of the seiner. The skiffs used initially were about 6.1 m long, 4.6 m wide and 1.2 m deep and constructed of plywood sheathed with fibreglass. To allow the skiff to pass freely over the corkline, tapered skegs are attached parallel to a tapered keel, and the propeller is caged. A heavy steel plate on the bow, with eye attached, provides great strength for hoisting or towing. A towing bit made of steel pipe is mounted amidships, securely fastened to the keel, and braced.

Propulsion is provided by a diesel engine, power varying greatly with size of the skiff and individual preference. Engines in early skiffs were between 75 and 150 hp. Considerable power is required during the towing operation, when the skiff tows the seiner on 91 m of 1.9 cm nylon line and keeps it from being pulled over the net during pursing and hauling. A 15.4 cm vertical gypsy is driven off the engine and used for pursing corks and manoeuvring the brail during transfer of fish from another vessel.

A rubber hose of 25.4 cm is fitted over the skiff rail to provide a friction surface for webbing that is pulled over it during sacking-up and also to act as a fender and to provide footing.

Later conversions

Later conversions incorporated features to increase safety and fish capacity. Watertight spaces were built under the turntable (C, in fig 3) to increase buoyancy in bad weather.

In still later conversions, the turntable was eliminated and a raised net platform substituted (D, in fig 3) combined with a completely enclosed watertight lower deck, increasing both safety and capacity. Extra fish wells were sometimes installed under the platform. The purse winch was installed on the raised deck. Fish are lifted to the raised deck and unloaded into hatches that lead to hoppers and distribution chutes between decks.

The fishing operation

Preparing the gear for a set. When a turntable is used, the net is stacked in three parallel piles running athwartships, the corks on the port side and the rings on the starboard. To start the stacking operation, a line is passed over the power block and snapped to the "triangle" end bracket of the hauling end of the net, which is then pulled through the block. The triangle is hung over the stern of the turntable, and the crew spreads out across the after end of the table to stack the net.

A line is passed through the rings as they are stacked and used later as a leader for threading the purse cable. About half the net is stacked in the first of the three piles (closest to the stern), which reaches a height of about 2.1 m. To start the second stack, the main boom is raised, bringing the power block forward. The second stack is allowed to reach a height of about 1.5 before the third is started. The third stack reaches a height of about 0.6 m. The incline yielded by the three different sized stacks is useful in bringing the seine skiff aboard atop the net (after the turntable is rotated).

The turntable is rotated to setting position with a cable from the pursing winch and secured with a pin set in a deck socket.

Next the seine skiff is lifted to its position atop the net pile with a 10 T capacity double block on the main boom. The following description of the hook-up is quoted from McNeely (1961):

> "The end of the seine towing cable is pulled from the winch towing drum, passed through the towing block, and connected to the hauling end "triangle" bracket. The purseline is then pulled from the winch, passed through the stern purse block and tied to the purse ring threading rope. The purseline is pulled through the rings . . . a sufficient distance to allow connection to an intermediate hauling cable which is coiled inside the skiff. A long link on the end of the purseline is then connected to a purseline release on the bunt end "triangle" bracket. The next step is to secure the intermediate hauling cable to a cleat near the amidships rail on the starboard side of the skiff."

On the fishing grounds, the skiff is shifted to the rear of the net pile. A steel cable painter is shackled to the bow of the skiff and secured to a pelican hook mounted on the winch. Safety is provided by a pin in the pelican hook.

Setting the net. When fish are sighted the pin is removed from the pelican hook, and when the signal to "Let her go!" is given, the hook is opened with a hammer, allowing the skiff with the net end attached to drop into the water. The skiff acts as a sea anchor and pulls the first portion of the net over the stern. Pull on the skiff is controlled by varying tension on the purseline with the pursing winch.

The set is controlled by the "fishing captain" on the mast or by an observer in an aircraft. The turning rate and speed of setting depend on behaviour of the school of fish. If the circle that can be completed with the net alone is too small, a larger circle can be made by letting out excess purseline and towing line.

When the vessel approaches the skiff at the completion of the circle, engines are reversed to bring it to a stop, and a heaving line is thrown to the skiff. The heaving line, which is secured to the forward purse block, is attached to the intermediate hauling line in the skiff, whereupon the hauling line and net end are released from the skiff, leaving it free to patrol the open water under the towing line between the vessel and the other end of the net, or, if no towing line is used, to take up its towing station at the opposite side of the vessel. The intermediate hauling line is passed through the purse block to a gypsy that is used to pull in the bunt end of the purse-line and the end of the net, which is attached to a steel hook on the davit. The purseline is then connected to the winch, and the release connecting it to the "triangle" is opened, freeing the purseline from the net end, so that pursing can begin. The bow breastline, after being disconnected from the "triangle", and the cork purseline are secured to cleats along the port rail of the bow.

Meanwhile, the towing line and purseline are being hauled by the winch. When all the towing line is in, the skiff commences its towing operation from the starboard side, attempting to keep the vessel square with the net and from being pulled into the net during pursing. When the towing line is in, the stern "triangle" is attached to a second retaining hook on the davit, towing line is disconnected and wound up on the winch.

The net is pursed until the rings are together and begin to come out of the water. Then the hoisting line, which was previously passed over the power block, is connected to the hauling end "triangle" and the end of the net is hoisted about 4.6 m in the air, away from the purse davit. A retaining line is placed around the netting to remove it from the port rail area so that the rings may be brought aboard. The following description of the handling of the rings is from McNeely (1961):

> "As the purse rings come out of the water, cable clamps, joined by a short bridle, are fastened to the purseline and hooked to a double block hoist located on the main boom. Cable is then slacked off the purse winch drums, and the purselines are removed from the purse blocks. The rings, dropper chains, and leadline are then hoisted high in the air. When these are well above the vessel rail, they are lowered slowly to the deck. The rings are then separated into four or five successive groups and tied with retaining chains which are permanently attached to the starboard rail. This prevents their being dragged back into the water.
>
> "Three snatch blocks are then employed to return the purseline, which had been wound up on the starboard winch drum, through the rings and back to the port winch drum. Two of the blocks are attached to the purse davit and one is located near the deck on the forward and starboard side of the turntable base. When this has been completed and the purse rings are free of the purseline, hauling of the net proceeds. Another method used to free the purse rings from the purseline, which results in a saving of time, is to open "figure eights" or split links, remove the line, and reconnect the ends. Twists in the purseline are also removed at this time."

Hauling the net. When the purse rings are free, hauling of the net begins. The retaining line is loosened, and the hauling end is pulled over the power block with the hoisting line. The purse rings are released in groups of two or three and, individually passed over the block, are retrieved, and threaded on a line. The purseline is inserted later as described above.

Now the net is dried up (hauled and stacked) until the area occupied by the fish is minimal. Excessive weight in one area may necessitate pursing the corkline. This operation is described in "Porpoise Fishing". If the catch is estimated to be very large (over 40 T), it may be split into two or three lots by pulling one or two "zipper lines". The skiff, its towing duties completed, comes alongside and picks up the corkline at the outboard side of the area containing the fish, forming a pocket. The fish are concentrated by further hauling of the net, and the corkline is secured fore and aft to both the vessel and skiff.

The "sack" or bunt is dried up further by strapping aboard 4.6 m sections of webbing with a winch power, using slings. When a section has been lifted, it is secured with a choker line pulled tight by the cargo hoisting drum or a gypsy on the winch, to prevent it from slipping back into the water. This operation is repeated until the fish are concentrated in a compact bag at the surface.

Brailing. The following description of the brailing operation, which follows "sacking up" is from McNeely (1961):

> "The small boom, used principally for brailing, is then vanged into the most advantageous position for handling of fish during the brailing operation.
>
> "The brail with hoisting sling attached is then lowered to the skiff men who guide the brail vertically down along the side of the skiff. The skiff men signal the winch operator to lower or hoist the brail by using a small police whistle or voice and hand signals. A 2 in (5 cm) diameter aluminum handle 16 ft (4.9 m) long on the brail allows the skiff men to guide the brail into the fish. When the brail is in position to take a full scoop of fish, the winch man is signalled, and as the brail is pulled up through the fish, the skiff men guide it to the side of the seiners until it emerges from the water full of fish.
>
> "A third man in the skiff holds tension on a brail purseline made of small chain until the brail is positioned over an unloading hopper. He then releases tension on the brail purseline, which opens the bottom of the brail bag, allowing the fish to spill into the hopper. When the brail is empty of fish, the chain man pulls on the brail purseline which closes the bottom of the brail and helps return it to the skiff men. The operation of brailing is repeated until all the fish are removed from the bag.
>
> "Fish deposited in the hopper are guided to selected brine tanks by a series of sheet metal chutes."

After brailing is completed, the strapped down webbing is released and the corkline unlashed from the vessel and skiff rails, and hauling and stacking is resumed until all the webbing is out of the water. Before the end of the net goes through the power block, the cork purseline and breastline are retied to their original attachment points, to the breastline and to the "triangle" respectively, and the hoisting line is attached to the "triangle" so that it may be passed over the power block for use during the next set.

1961–70 EXPANSION AND NEW CONSTRUCTION

On the heels of mass conversion of bait-boats to purse seiners began a decade that further revolutionized the tuna purse seine fishery. The fleet of today is dominated by newly-built, large capacity seiners, vessels from 42.4 m to over 76 m long. These seiners are moving into new areas of fishing with new fishing tactics, modern gear, and increased efficiency.

Technology

The most distinguishing characteristic of the purse seiners since 1960 is their size. Before 1961, the largest seiners (converted bait-boats) were of about 591 t carrying capacity. Only two were larger than 455 t and the average size lay somewhere between 182 and 273 tons.

Since 1961, 38 new purse seiners, including nine conversions from military hulls, have been added. The largest of these vessels is nearly 829 t and the average size is 655 t. Typical purse seines of this period are shown in figs 5 to 8. The total capacity of these seiners, at the end of 1969 (23,268 t) comprised 52 per cent of all U.S. purse seiner capacity (44,674 t, 120 vessels). Forty-three bait-boats represented an additional 3,710 t of capacity (Inter-American Tropical Tuna Commission, 1970).

Several other tuna purse seiners are (in 1970) under construction in San Diego, California and Tacoma, Washington. Among these is one of 1,820 t carrying capacity, nearly twice the size of the largest tuna purse seiner now in existence.

TABLE 2. ADDITIONS TO U.S. PURSE SEINE FLEET EXCLUSIVE OF BAITBOAT CONVERSIONS, 1961 TO 1970

Year built or year converted from military hull	*Number of vessels added*	*Added capacity as of 1969* t
1961	3	1705
1962	4	2415
1963	4	3425
1964–1966	3	1769
1967	2	1360
1968	7	5003
1969	13	7375
1970*	2	1592
Totals—	38	24819

* As of 13th March.
Source: Unpublished data of the Inter-American Tropical Tuna Commission.

Increasing size within reasonable limits offers a number of advantages which may help improve profitability: as vessel size increases, cost of construction per ton of capacity decreases, as do many operating costs. The ratio of fishing time to travel time increases with vessel capacity and, of course, large vessels are more seaworthy and have greater range than smaller vessels. At some point in size, depending on conditions of operation, these advantages are offset by the drawbacks of practical limits on net size, crew size, school size of tuna, length of trips, and other factors which tend to increase operating costs per ton of fish caught.

Many owners of small purse seiners are prevented from buying larger, more efficient vessels because of the lack of a market for their older boats. One fleet-owning corporation, after an analysis of optimum sizes of purse seiners (Green and Broadhead, 1965) found a way out by enlarging existing vessels. Over a period of four years, seven steel-hulled purse seiners were cut in two near amidships and sections spliced in to lengthen them by 14 ft to

32 ft (4.26 to 9.7 m) (fig 9). Carrying capacity was thus increased by 73 to 164 t. The changed length to beam ratio also improved speed by about ½ kn and sea-keeping ability. All seven of these vessels were of about 309 t capacity before the operation. They are said to be rapidly paying off, through increased efficiency, the cost of their modification.

Hull design and general arrangement of the first new purse seiners differed little from the familiar tuna clipper of the past. Since that time, new construction has been marked by occasional innovations and establishment of new trends until the seiner of today appears quite different from early conversions. Externally, several new seiners stand out sharply.

Arthur DeFever, designer of several new vessels says: "The seiner of today, which is noted by its rakish bow, conically shaped stem head, tapering to a fine entrance at the water line, appealing bow flare, forward-look side panels, modern superstructure, streamlined stack and slightly curved sheerline with low point near the stern, is good looking, and except for her seine net and skiff on the stern, she has a somewhat modern research ship appearance, or even scaled-up yacht aspect."

Fig 9. Lengthening a tuna purse seiner. Photo courtesy of National Marine Terminal, Inc.

Wooden hull construction, once predominant in the tuna fleet, has been entirely replaced by steel in new construction. A stern ramp for carrying the seine skiff for immediate launching avoids carrying the skiff on top of the net and semi-launching it on the grounds. The older method results in an actual towing situation, slowing the vessel's speed and restricting scouting operations, as well as causing wear and tear on the skiff. The seine skiff, itself, has kept pace with the development of the modern purse seiner, especially with respect to size. The skiff on one of these purse seiners may be 10 m long with 5.8 m beam and weigh 12.7 t. On some, a skin-cooled engine of 300 hp drives a 1.2 m diam. propeller through a 4½:1 reduction gear, others use twin diesels for power. The vertical gypsy, used for pursing floatline-ropes, is hydraulically driven (Arthur Yeend, personal communication).

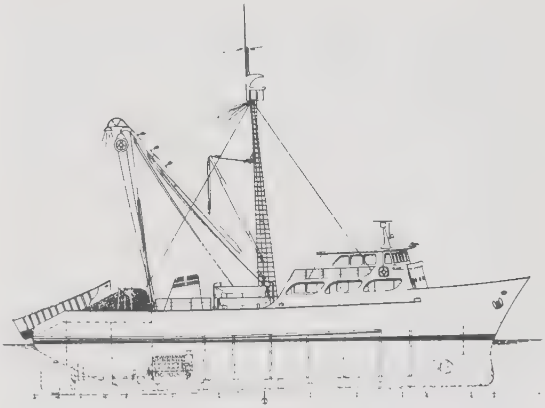

Fig 10. Outboard profile of purse seiner type of Vivian Anne. *Note in particular the bulbous bow, bow thruster, short drive shaft, and that the fish holds are forward of the engine space (After DeFever, 1968)*

Atop the bridge on several vessels may be found a small helicopter landing pad. Beneath the water line some include a bulbous bow for increased speed and a bow thruster for improved manoeuvrability while in the set. This latter may even be controlled through the autopilot, so that the seiner can maintain a constant heading even while dead in the water (Arthur Yeend, personal communication).

Control of vessel and gear during fishing operations has been simplified by consolidating most control operations into several strategic stations. The "fishing station" is now a standard, built-in convenience. It has an auxiliary set of full controls on the port bridge wing which permits the skipper to operate the vessel while looking down at the deck working area and out over the net. The hydraulic control console for the operation of nearly all of the after deck hydraulic machinery and power block is mounted in a position where the operator has full view of operations on the working deck. Seine winches may be separated for best locations of main functions and for easier maintenance. For example, the towline winch may be separately mounted on the port side in line with the setting of the net, thus eliminating one fair lead on the seine davit (Sverre Jangard, personal communication). The crow's nest may be fully outfitted and carry up to three men. From here, the mastmen, besides scouting for fish, may direct the operations of porpoise chasers by citizens band radio as well as coordinate deck operations with fish movements within the net, communicate with other vessels or spotter aircraft, or by way of another auxiliary set of controls, operate the vessel during the set.

Stern engine rooms (fig 10) with either single or twin main engines are included in several new boats by different builders. This arrangement offers the advantages of better weight distribution; short, one-piece tail shifts, and more efficient utilization of space (DeFever, 1968). Stacks are either offset to starboard on the aft deck just forward of the net platform or ducted forward to the more conventional stack location aft of the pilothouse. Skin-cooling, through the seiner's hull may be used instead of conventional heat exhangers (Arthur Yeend, personal communication).

While the power range of the older purse seiners was about 200 to 1200 hp, there are now purse seiners of 3200 hp or more. Many of these newer boats can sustain speeds of 15 kn, compared to older average of 10 kn.

Conventional ammonia refrigeration through brine is still employed although somewhat improved by the use of smaller wells (40 t capacity) with dual ammonia circuits in each well. Larger wells may have three circuits. Unloading is facilitated with more and larger unloading hatches.

Aft of the bridge deckhouse and on the after working deck is ample stowage room for up to three porpoise chaser boats ready for launching on their hydraulically-operated davits.

The modern purse seiners equipment may also include fuel oil centrifuges, hydraulic steering and pneumatic controls, and anti-roll devices. Included in electronic equipment is the newest Omega navigational system as well as the standard array of modern communications systems, radar, Loran, radio direction-finder, automatic pilot, echo sounders, and sometimes sonar.

Larger fishing vessels require longer trips to fill their capacity. Trips of long duration may adversely affect crew morale and therefore lower efficiency. Designers and builders have realized this and have designed modern tuna purse seiners with the comfort and morale of their crews in mind. Quarters are pleasant and well-appointed and may have built-in hardwood bunks and cushioned settees, ample closet and stowage space, carpeting and ample lighting. A stern engine arrangement makes all living quarters extremely quiet. Several toilets with stall showers and hot and cold water may be available for the crew with private toilets for the captain and engineer. Fresh water makers and ample water storage space have eliminated the water shortages of the past. A spacious, airy galley and dining room with large windows on three sides gives almost the impression of a fine waterfront restaurant. All living quarters are air-conditioned and some vessels even have high fidelity music piped to the various rooms.

Purse seines and related gear

American tuna purse seines have changed little except in size for the last ten years. A typical purse seine at the start of this decade was 420 fm (765 m) long by seven 100-mesh deep strips of netting (McNeely, 1961). Nets carried by the newer purse seiners may be over 600 fm (over 1100 m) long by ten strips deep. While No. 42 thread (3543 Tex) is still used mostly in the main body of the net, some of the larger nets used when fishing tuna associated with porpoise are going to No. 48 and No. 54 (3720 and 4022 Tex).

Interest in tuna purse seine research has been stimulated by the Bureau of Commercial Fisheries development of the Hybrid Tuna Purse Seine. This experimental net features lighter webbing, lower hanging coefficients, tapered wings, floatline/leadline ratio = 1, gavels with breast pursing lines, and a setback of main purse rings from net ends. It has been very successful on "school fish" tuna, especially where erratic fish behaviour makes successful purse seining difficult. A complete report of this experiment is given elsewhere in this volume (Green, Jurkovich and Petrich).

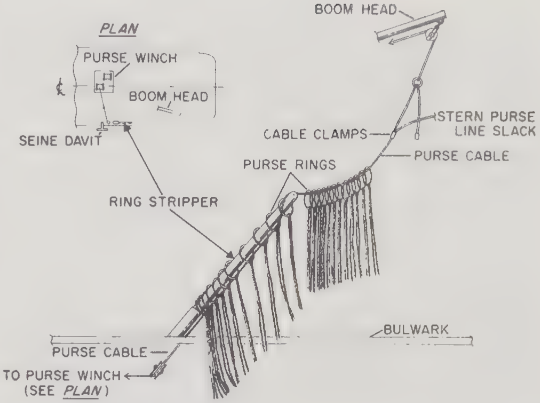

Fig 11. Ring stripper just before purse rings are placed on it. Drawing courtesy of Morris Whaley. Drafted by Kenneth Raymond

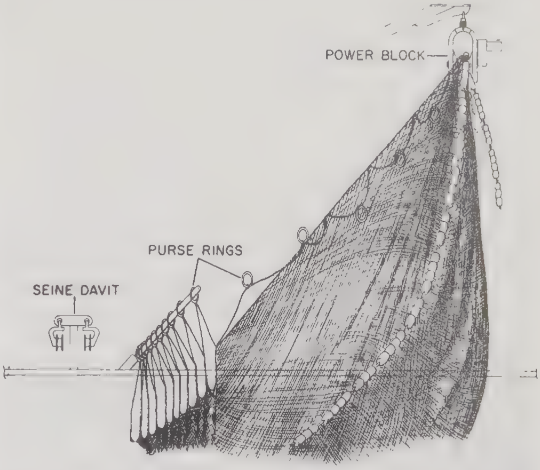

Fig 12. Ring stripper. Purse rings are pulled off as net is stacked. Drawing courtesy of Morris Whaley. Drafted by Kenneth Raymond

There have been tendencies in new net construction of the last few years to introduce tapers in the wings and to be more generous in hanging in webbing, using hanging coefficients as low as 0.82 as opposed to the standard of 0.91 of ten years ago.

Net handling gear has remained essentially unchanged with the exception of the purse ring stripper, a patented method of handling the purse rings so that they and their bridles and the leadline do not obstruct working deck space or create a hazard during net stacking. The purse rings are, instead, threaded onto a steel shaft which is mounted rigidly just aft of the seine davit on the port bulwark. The operation of this device is as follows: the purse rings are hauled up to the seine davit and lifted with cable clamps from a double block hoist on a cargo boom in the usual manner. Now, instead of dumping rings and chain onto the deck, the bow portion of the loose purseline is placed in a groove running over the end of the shaft of the ring stripper. Tension is transferred from the bow cable clamp to the bow purseline running over the ring stripper and the bow cable clamp is removed so that the rings are now hanging in the bight of the purseline between the end of the ring stripper and the stern cable clamp. This clamp is lifted until the rings slide forward on the purseline and spill down over the ring stripper (fig 11). The purseline is now removed from them as usual. The ring stripper is mounted at such an angle that, as the net is stacked, the rings are pulled off singly by the power block (fig 12) (Morris Whaley, personal communication).

"Porpoise fishing"

American tuna fishermen in the eastern tropical Pacific depend on porpoise for locating much of their fish (Perrin, 1968). Schools of yellowfin tuna usually occur in close association with large schools (up to 1500 animals) of two species of porpoise, *Stenella graffmani* (called "spotter" by the fishermen) and *Stenella longirostris* (called "spinner"). Because porpoise are air breathers and stay at the surface, the fishermen can spot them more easily at a distance. About half of the seine-caught yellowfin tuna from the eastern Pacific is captured from schools associated with porpoise (data furnished by Inter-American Tropical Tuna Commission). Yellowfin tuna make up approximately half the U.S. tropical tuna catch; the remainder is mostly skipjack (*Katsuwonus pelamis*).

The reason for the association of tuna and porpoise is unkown (Petrich, 1965) although some food-based relationship is suspected. Stomach-content analyses thus far carried out are inconclusive but indicate that they feed on some of the same things.

A new aspect of the tuna-porpoise association came to the fore when purse seiners began to replace pole-and-line boats in the tropical tuna fishery. The fishermen discovered that the association is very tight. They found that the fish seem to follow the porpoise very closely and that they can be herded by herding the porpoise, and that if even a few porpoise escape from the circle of the purse seine, all the fish might follow and be lost. These discoveries led to the development of a unique method of operations, called "porpoise fishing".

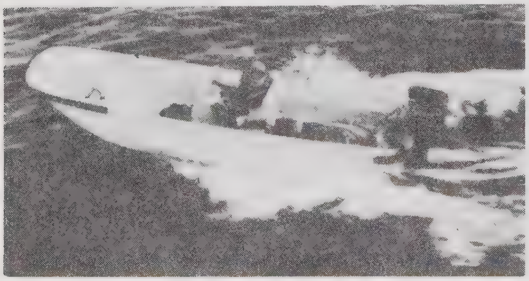

Fig 13. A light, powerful combination of skiff and engine is used for chasing and herding the porpoise. (After Perring, 1969)

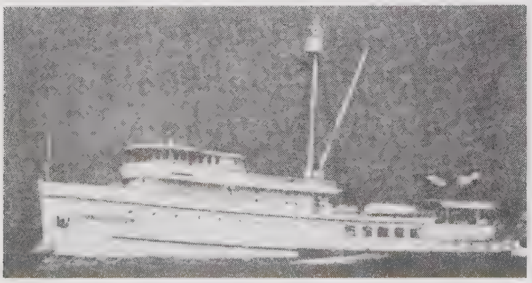

Fig 14. Seaplane lashed to canopy of tuna clipper Constitution. *Photo by Allied Craftsmen, courtesy of Vernon M. Brown*

The fishermen spot porpoise schools at the horizon with high-powered binoculars (up to 20 power) sometimes mounted on swivelling racks on the bridge. Most boats carry two such sets of binoculars. While the boat is on the tuna grounds, a constant "spotting watch" is kept during daylight with crewmen rotating the duty. In addition, a lookout with less powerful binoculars is posted in the crow's nest.

Feeding schools often can be detected over the horizon by sighting the birds (terns, boobies and frigate birds) which gather over them. When a school of porpoise is sighted, the boat runs up on it while the lookouts scan it for signs of fish. If the lookouts spot numerous "jumpers" (feeding fish breaking the surface), "shine" (flashes of reflected light from fish below the surface), or see a "blackspot" (dense school of fish below the surface), the boat prepares to set. If no fish signs are seen, the captain may still decide to set, gambling on the presence of unseen fish.

The boat stops, and the "chaser-skiffs" (also called "speedboats" or "pongos") are lowered overboard. These boats herd and direct the porpoise, slow them down if they are running, and tighten up the school. Most large seiners use two chaser-skiffs. A popular combination of skiff and engine is a 4.8 m fibreglass tri-hull using an 85 to 105 hp outboard motor. The skiff drivers are strapped in their seats and wear crash helmets (fig 13).

A "cork tender", a smaller skiff, is also lowered. This skiff follows the boat during the chase, and its driver tends the corkline during pursing and hauling.

The "fishing captain" (who may or may not be the boat captain) directs the chase and set from the mast. He has two-way radio contact with both chaser-skiff drivers.

Making a good set on porpoise is a fine art, and good "fishing skippers" are in high demand in the tuna fleet. The fishing captain directs and uses his chaser skiffs like shepherd does his dogs. When the school is headed properly, the captain sets his net.

When pursing is completed, the fish can no longer escape. Now the problem remains of separating the unwanted porpoise from the valuable tuna. For this purpose fishermen have developed an operation called "backing down". At the front end of the net (the end which goes overboard first, attached to the seine skiff) are several 30 fm lengths of line strung through 10 cm rings attached to the corkline by 0.9 m bridles. As soon as the front end of the net is picked up at the completion of the set circle and secured to the pursing davit, the man in the cork tender passes three or four of these lines to the deck, and they are pulled with the bow winch and secured.

This action causes the corks to bunch and a "balloon" to form in the back of the net. The net is then "dried up" (taken aboard) to approximately "half net" (farther if the catch is small). The net is strapped down, the rings are secured, and backing down begins. The fishing captain directs from the mast. When the fish are near the boat and the porpoise at the far end of the net, he gives a signal, and the boat backs down, opening the net and at the same time sinking the corks at the far end.

Most of the porpoise are spilled over the corkline. The fish tend to swim upcurrent and into the balloon formed by bunched corks. Great care must be taken to avoid losing the fish as well as the porpoise. If the fish head toward the end of the net, the captain signals, and the engines are immediately put into forward allowing the corkline to rise to the surface. The cork tender is stationed at the end of the net to assist porpoise over the corkline.

After the backing down, the net is dried up to the bunt (reinforced section at the back of the net). The bunt is "sacked up", that is, webbing in excess to that needed to hold the fish is gathered up from the bottom and tied down. The seine skiff comes alongside, and the corkline on the side of the "bag" opposite the boat is secured to the skiff's rail. A portable rack is hung on the skiff, and a crewman stands in the rack and assists the remaining porpoise over the corkline. The bag is then sacked-up farther, and the fish are brailed aboard.

The Bureau of Commercial Fisheries has in recent months begun research to develop improved methods of eliminating mortality of porpoise in the fishing operation.

Fish finding

Visual scouting, whether it be from the bridge, crow's nest or aircraft, is still the most important method for finding tuna in this fishery. After a fishing area is chosen by experience with seasonal movements of fish, current contacts with other tuna boats, etc., all available crewmen act as lookouts whenever the vessel is on fishing grounds. During daytime they search from vessel to horizon with high-powered binoculars or with the naked eye for such signs as birds, whales, porpoises, basking sharks, floating objects or surface disturbances from tuna. If night fishing is done during the dark of the moon they search the water for bioluminescence caused by tuna presence. The glow may be intensified by stimulating the tuna to increased activity with occasional sweeps of a searchlight.

An airborne observer can be a useful adjunct to the fishing operation in two ways: (1) he can spot fish at great distances from the vessel because of the aircraft's height and range of operation. Under ideal conditions (sun overhead and clear skies), an observer flying at 182 m can scan a swath of ocean 60 miles wide as compared to 19 miles for an observer in the vessel's crow's nest at 18.2 m, having a good view of the fish and their position relative to the vessel, or to the porpoise school in the case of "porpoise fishing". (2) He can "set the boat", telling the vessel when and where to release the net and how to manoeuvre in completing the circle of the set.

The first use of a ship-based aircraft in the tuna fishery was in 1946. A helicopter (Sikorsky S-55) was taken out on the *Espiritu Santu*, but proved too expensive to maintain (personal communication from Robert Jones). In the 1940's some boats began to carry small seaplanes (fig 14). By 1952, 21 seaplanes were in use in the fleet, but a period of economic hardship cut the number until by 1955 there were none left.

In the early 1960's, after conversion of the fleet to seiners and after economic improvement, interest in ship-based aircraft was renewed, and since then helicopters have been in sporadic use, two or three being in operation every fishing season. In very recent years, with the advent of very large seiners (546 to 1,900 t capacity), the use of a helicopter has become economically more feasible, and some new designs include built-in helicopter pads.

There are advantages and disadvantages in the use of both fixed-wing aircraft and helicopters. A helicopter has the great advantage that it can take off from and land on the vessel, but is expensive and extremely difficult to maintain properly, especially under at-sea conditions, and is easily crippled if forced to land in other than flat-calm seas conditions. A seaplane has greater range than a helicopter (up to 7 h) and is more dependable and economical to maintain, but it must be lowered into the water to take off and be picked up after it lands. If a simple method of launching and recovery, perhaps with a special large boom, could be developed, the seaplane, because of its range and dependability, would seem to be the better-suited craft for use at sea. The chronic problem of rapid metal corrosion due to prolonged exposure to salt-laden air could easily be eliminated aboard the large vessels through a system for washing down with fresh water.

The use of shore-based aircraft spotting services has proven more cost effective than maintaining aircraft aboard ship. A percentage of the value of fish caught with such assistance is usually paid to the spotter pilot. The service is limited, however, by the distribution of adequate shore facilities and the range of the aircraft used.

Sonar has seen little use in this fishery. Of the few purse seiners carrying it, we know of no one who uses it for making sets on tuna. Our fishermen, inexperienced with this gear, are loath to make sets on anything whose species or size cannot be identified. A set on a school of mackerel or undersized tuna may result in a "christmas tree" (purse seine loaded with gilled fish).

Several seiners have had navy surplus, bathythermograph (BT) winches installed in a cooperative research project with the Bureau of Commercial Fisheries. BT data collected during their fishing operations established a direct relationship between the depth and temperature gradient of the thermocline and the success of purse seine sets (Green, 1967). This fact has been increasingly used in searching tactics for tuna. The use of the more modern expendable BT system is now beginning to replace the older mechanical type.

Automatic water temperature recorders with read-outs conveniently located in the pilot house are replacing the use of the engine room water intake temperatures for fish scouting. All tuna fishermen have learned through experience the optimum sea surface temperature ranges of the tunas that they fish for and use this knowledge in their scouting tactics. Temperature changes are used to locate oceanic "fronts"—lines of convergence of different water masses. Tuna fishermen often follow these fronts as they scout for fish.

Expansion of the fishery

Along with technological development of the American tuna purse seine fleet in the 1960's has come major changes in the distribution of production centres and fishing areas.

Production centres. As late as 1953, the southern California canneries accounted for 87 per cent of the national pack. In recent years the situation has changed due to the attraction of processors and vessels to Puerto Rico. Processor interest in Puerto Rico stemmed from availability of low cost labour, proximity to eastern markets, and tax incentives. In 1953, tuna canning operations started in Puerto Rico with the establishment of one packing plant. At present, four canneries operate there.

As canning in Puerto Rico increased, tuna vessels from southern California transferred there also. The logistics of operating there, however, favoured only the larger vessels. In 1958, ten bait-boats with a combined capacity of 3,840 t, 11 per cent of the total U.S. tuna fleet's capacity (both bait-boats and seiners), were based at Puerto Rico. Since 1966, an added incentive to the large purse seiners has been the proximity to the burgeoning tuna fishery off the west coast of Africa. In 1969, 21 purse seiners totalling about 15,015 t capacity or 31 per cent of the total fleet's capacity were based there. Of these, 15 vessels were among the new additions to the fleet since 1961 (section 4.1.1). At present, no U.S. bait-boats operate from Puerto Rico.

Of the U.S. total annual tuna pack in 1967, Puerto Rico produced about 32 per cent, southern California 44 per cent, the rest of the continental U.S. 12 per cent and American Samoa and Hawaii 12 per cent (Forbes, Stevenson and Baldridge, 1969).

Regulations and shift from eastern tropical Pacific. In 1966, for the first time, conservation measures for yellowfin tuna in the eastern tropical Pacific recommended by the scientists of the Inter-American Tropical Tuna Commission (IATTC) were adopted by member nations. These recommendations included a "catch quota" (72,163 t in 1966). That year the closure date was September 15. After this date, no vessels were to leave port to fish yellowfin, but more than 75 per cent of the fleet was still at sea, unloaded, and fishing therefore continued in almost full swing for most of the rest of the year.

In 1967, however, the closure date was June 24th, and the fleet suddenly found itself faced with the alternatives of fishing exlusively for skipjack or going farther afield in search of yellowfin outside the IATTC regulatory area. Three vessels chose to seek yellowfin on the west coast of Africa in the Gulf of Guinea, where tuna vessels, mainly bait-boats, of France and other nations, have long operated. The three vessels, the *Caribbean*, the *Southern Seas* and the *Day Island*, fished as a group and shared the spotting services of a helicopter (Simmons, 1968). About 1,365 t of tuna were caught in two months of fishing (unpublished data furnished by IATTC) including 81 t of yellowfin "on porpoise" (*Delphinus delphis*).

In 1968, the closure date again came in June, and spurred by the success enjoyed by the three vessels that visited Africa the previous year, eight vessels went to the Gulf of Guinea. In 1969, closure came even earlier, in April, due to the increased capacity of the fleet, and 23 vessels went to Africa. In 1970, closure came in March, and the fleet is still larger, so the move to the Atlantic can be expected to be still greater.

Some vessels of the U.S. fleet have begun fishing far offshore, outside of the regulated area after the closure of the yellowfin season. Interest is being shown in other areas, including the Indian Ocean and the central and western Pacific Ocean. A cannery-financed exploratory trip, in the latter areas, by one purse seiner was carried out in the summer of 1970.

PROSPECTS FOR THE FUTURE

Total world demand for tuna has increased rapidly in recent years. World consumption of tuna and tuna-like species (in round weight) increased from 0.99 million t in 1958 to 1.4 million t in 1968 (FAO, 1969). *Per capita* consumption of canned tuna in the U.S. has increased from an average of 0.49 kg to 1.1 kg reported in 1969 (Forbes, Stevenson and Baldridge, 1969). This rising trend is expected to continue at a higher rate because of increases in population and, more importantly, standard of living.

Bell (1969) estimates that world consumption of tuna would double in each of the next two decades if supplies are adequate and there is no rise in prices. He estimates, however, that the world's oceans can supply only about 2.6 million t of tuna on an annual sustainable basis, and that prices and costs of tuna will double by 1990, with a world catch of about 2.1 million t, and triple by the year 2000 when the world's maximum sustainable yield is reached. This assumes that overfishing will be prevented as each of the stocks are exploited.

The American tuna fleet, since its inception, has been constantly responding to both foreign and domestic developments affecting their operations and markets and will continue to do so. The present trend to new construction of large purse seiners shows no signs of abatement. At the end of 1970, total U.S. tuna fleet capacity will be about 58,695 t. While many of these larger vessels are designed with the potential of worldwide operations in mind, it must be expected that they will also compete with the smaller, older vessels on the closer, traditional fishing grounds of the eastern tropical Pacific. With the entry of the newer vessels in this fishery, and the yellowfin season being progressively shortened, many smaller boats, which have no other place to fish, may be forced out of business as competition is intensified.

Expansion of the newer vessels of the U.S. fleet into waters outside of the yellowfin regulatory area, however, is certain to continue. Prospects may include the central and western Pacific Oceans and Indian Ocean. Catch per unit of effort cannot be expected to remain as high as present levels as new resources, such as central Pacific skipjack are relied upon. Although the stocks of these fish may be high, they are diffusely distributed, and with present technology, difficult to find and harvest. Production costs will therefore increase.

Competition from foreign tuna fisheries, using lower cost labour, is apt to increase. Japan, now experimenting with purse seining for tropical tunas in the eastern Pacific may decide to enlarge that segment of her long-range tuna fleet. Ecuador is proceeding with plans to build a tuna purse seine fleet with financing from the United Nations' International Bank for Reconstruction and Development.

In spite of developments of the past ten years, purse seining methods and gear have remained basically the same. But, with longer-range operations, higher production costs, and competition with low-cost labour, the U.S. fleet may be forced to raise its level of technology in the years to come. Improved refrigeration methods and partial processing at sea may be able to increase the value of the catch. Loading the catch aboard should become more mechanized to avoid loss of time on the fishing grounds and similarly more mechanized off-loading, such as containerized fish holds, can reduce turn around time by as much as two to three days. Diesel electric or turbine electric main drives should be considered (DeFever, 1968). Net handling may be improved by developing methods of mechanized net stacking. The use of articulated cranes instead of the old style mast and boom rigging may further speed the fishing operation. The purse seine, itself, has only recently come under scrutiny for possible improvements in design (Green, Jurkovich and Petrich, 1970). Methods for quickly changing the hang-in percentage and depth of nets are waiting to be tried (Petrich, 1968). Nets, in the future, may be of more highly specialized designs for particular fishing conditions.

As tuna inevitably become scarcer we must expect to develop and improve scouting and fish finding methods. Sonar may eventually play a more important role in the U.S. tuna fleet. We may expect to see refinements in the use of ship-based aircraft including the development of airborne, automatic sensors. Work has already begun in the use of satellites to locate fishing areas.

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[R.E. Green, W.F. Perrin and B.P. Petrich]

7109

VESSEL TECHNOLOGY

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I am going to talk about technological innovations for the San Pedro wetfish purse seine operation that can perhaps increase the efficiency and reduce the cost of the operation. I would like to begin by going into the general problem of making money with a fishing boat or for that matter with any production business. In order to remain competitive, that is stay in business, one has to, if it is in an expanding economy, manage to increase productivity in line with the increase in cost of operation in order to cover the increase in labor costs that have to go up in an expanding economy. This increase in labor cost has to be offset either by reducing the operating costs of the business, by increasing the dollar value for its product per man hour, or by raising the prices.

Before we look at the fishery, let's look in general to what has happened in the American economy over the past decade. In general, the indices of the agricultural product have gone up some 15%. The wholesale price indices have risen similarly; these are, I believe, something on the order of 20%. In general the cost of living has gone up some 30–35%. Now if we look at a fishery, it is obvious that the vessel operator is going to have to keep his unit producing fish at a price in keeping with the levels of the wholesale price indices. The fishermen, however, have to increase their wages someplace in keeping with the cost of living index.

The high seas tuna fleet has in general followed this type of tendency. Productivity in fish/man hour and boat year has risen in the last decade allowing an increase in the crewmen's wages and owner's profit. However, if you look at Bill Perrin's data on the San Pedro wetfish fleet, you will see productivity in this fleet has stayed essentially level over the last decade.

If the position of the San Pedro wetfish fleet is to improve, somehow or other, the productivity of this fleet is going to have to go up. Jack Baxter showed that it is possible to pull about $5 million worth of fish out of the southern California ocean without any major changes in the fleet. Right now it is only about 2½ million. We have a pretty good chance to increase the landings if we can overcome some of the obstacles that, in the past, have kept the production down to about half of what it could be.

Increasing the productivity of the fishing fleet can be done in two ways, or a combination of these two ways. You can increase the value of the catch or you can cut cost. Some of the problems that must be overcome in these two areas are legal problems: some deal with management in an economic sense—as in operating a fishing boat—and some with economics in the marketing sense—that is developing markets for these products. But also, some of these problems are technological in nature, that is, they require the application of engineering and science. It is these latter problems that I am going to discuss, but since there is some interaction between these categories, I will probably touch on all of these problems.

To start with, let's look at those actions that will affect the value of the catch. The most obvious way to increase the value of the catch is to raise the price of fish. This is, however, a marketing problem and one that technology cannot do very much about.

Another approach, you might use, would be to increase the volume of the catch; here we run into a number of subproblems. A portion of the cost of operating a vessel is "fixed" cost. Regardless of whether the vessel goes to sea or not you have to pay interest on your loan, you have to pay moorage, and insurance, etc. It is obvious that the more fish you catch the less the fixed costs will affect the production cost; but to catch more fish means that some existing obstacles must be overcome. For example, our San Pedro fleet has a list of, I believe, some 90 port rules that are mostly holdovers from the sardine days which say you cannot fish on certain holiday days, weekends, and during the full moon periods as well as other restrictions. The boats also are faced with certain periods of bad weather when they cannot fish. The overall result is that they are only fishing on an average of about 100 days a year. It would be desirable, when you are operating a vessel, generally to have it operate for 200 to 250 days a year. Unfortunately, technology cannot do anything about port rules or about labor problems, and at present we cannot do anything about the weather. There are however some things technology can do about increasing the volume of the catch by increasing the days of fishing per year. Part of the problem is that some of the fish are available at only certain times of the day. For example, there is a tendency for the fish to come up at night, disperse, go down deep during the day. They are only available to the fishing gear for a short portion of the evening and a short portion in the morning. If it were possible, for example, to fish during the daytime when the fish are still deep, this would essentially increase your time on the fishing ground and fishing time by probably twofold. It is possible in other parts of the world to fish deep schools using sonar and deep nets. Both sonar and net technology are well developed and there is no reason why they could not be applied here.

We have a third problem which restricts the volume of the catch and this is the legal barriers, the institutional barriers, that control seasons, fishing areas, the size limit of the fish, and in some instances the

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type of gear. Institutional barriers, in general, are not open to technological solution.

A fourth problem affecting the value of the landings is, what you might call, the dockside bottleneck. Generally in a fishery there is an optimum vessel size which makes the most money. This is not true, as you have just heard from Bill Perrin, in the San Pedro fleet. In a large part, I believe it is due to the limited capacity of the processing plants. In the tuna industry when fishing is good and you have a lot of vessels coming into port, you may have to wait several weeks to unload; since the high seas tuna vessels are refrigerated they can tie up at the docks and act as freezer plants for the canners. In the wetfish fleet, however, the vessels are mostly unrefrigerated and therefore, you cannot have them setting around more than a couple of days or someone will complain. So the processors are forced to put limits on what the boats can bring in; this is so they will not bring in more than the plant can handle. This often means that the vessel is allowed less than a full load and probably tends to hurt the bigger boats more than the smaller boats. This problem of limits may be a matter of marketing in that the processor can sell only so much of that species and that he wants no more. This may be a matter of economics; it may not be worth the money for the processor to increase his processing capacity or to meet some of the new standards of pollution control that have been put into effect in the San Pedro area. But I think it is also likely that partially it is just a matter of poor plant utilization—that there is a bottleneck at dockside. This is open to analysis and technological solution. For example, it is possible to hold fish in refrigerated sea water for periods of up to 10 days without appreciable loss in quality. It might be feasible to prepare several large refrigerated sea water barges that could act as accumulators for fish so that when fishing is good the vessels could unload at the barges and the plant could then spread out its capacity over a period of time. That might cover weekends when the vessels are not allowed to fish and it might cover bad weather periods. This type of accumulator system might have some additional benefits. It might be that these barges could also be used to transport some plant effluents offshore and dump them instead of the plant now being required to run a pipeline out past the Long Beach breakwater. It also might be that by providing this type of storage for the fish it would allow a continuous monitoring of the catch, for example, for some of these pollutants, pesticides, residues, and the processor could have time to decide whether or not a load of fish went into the can or whether it had to go to the reduction line. I don't know who would pay for this or how effective it would be, but it is a problem that can be studied and one can come up with some answers.

Finally, we can get into this concept of managing the vessels themselves, that I hoped Mr. Douglass would talk about. If the processors only want so much of each species and it costs so much to catch a pound of this fish at a certain time of year, and a pound of that fish at some other time of year, or if there is only a little bit of one species available and a lot of any other, it might be interesting to see if you could change the strategy of fleet operation. For example, you could assign different vessels to different species to meet the market demands. During the times when there is a small run of tuna, instead of allowing the entire fleet to go out and waste their time searching for these tuna you could assign the majority of the fleet to mackerel and let only a few boats fish for tuna. Then perhaps you could develop a management system whereby you could pool profit in part so that the boats that are fishing for the low value species would not necessarily have to suffer. Such an approach is open to modeling; it is part of the Lenarz/Perrin economic model and I think it will prove very interesting. I don't think, however, that it is a solution that is very easy to implement.

Besides increasing the value of the landings the second obvious way to improve the vessel productivity is by reducing the operating costs. Although this cannot be potentially as profitable as increasing the volume of the catch, I think it is a little easier to obtain at this point. It is certainly very important in a business sense. I can think of three ways to cut down costs: you can cut manpower, you can speed up the fishing operation, or you can reduce the overhead. With a fishing boat all of these are open to technological solutions.

To cut manpower you can mechanize the operation. Right now we have a subcommittee of the Marine Research Committee which is evaluating the cost effectiveness of mechanizing wetfish purse seining using a fish pump rather than the mechanical brail, operating the vessel without using a power skiff by using a side thruster or bow thruster instead of the seine skiff and by using a storage drum for the net rather than stacking the net in the net pile by hand. We hope that by using these three innovations these boats will be able to operate with a five-man crew rather than the nine or 10 men that are used now. We also hope that the capital cost of this mechanization can be recovered from the labor cost saving realized by reducing the number of men in the crew and taking some of the increased crew earnings, and applying it to the vessel share.

Speeding up the operation is in part a matter of technology and in part an institutional barrier problem. If the drum seine and the fish pump are successful, a considerable savings in the actual operating time in making the set should result. However, the biggest waste of time, in this and about any other fishery, is in finding fish. It should be possible to reduce search time by using sonar and by improving the forecasting and fish spotting services but I don't want to develop this theme any further.

Now we come again to the institutional barriers. In our area we have a problem in that the vessels are denied the right to fish inside the 3-mile limit and they are not allowed to fish in some other restricted areas. At present this results in considerable increase in running time. We have to live within these restrictions right now but in the future if they were somehow modified or changed I think it would probably do more to increase the profit to the wetfish vessels than any of the technological innovations.

The last item I want to develop is the reduction of overhead. One overhead item in the San Pedro fleet or in any fishing fleet is the cost of paying off your vessel. For the modeling purposes, we have used cost construction estimates in the quarter to half million dollar range from some of the new vessels that are being constructed. However, I recently talked to a couple of fishermen who felt that they could build a boat for our local conditions for less than $100,000. This would be essentially a flat bottom power barge which would pack 200–300 tons of fish. I think that this idea has some merit. The question is, is it economically sound and is it legally possible to build a vessel for wetfish that might not be sea worthy or readily adaptable to another fishery? But again, the question is open to study.

Well we have looked at most of the major problems that are holding back the productivity of the San Pedro wetfish fleet.

In summary, we want to accomplish two things: we want to increase the value and volume of the landings and we want to reduce the cost of catching fish. Increased value and volume through technology might be achieved by increasing the time a vessel can spend at sea, by using sonar and deeper nets, by increasing the plant capacity using this refrigerated sea water accumulation system and by developing a vessel operations strategy for a multi-species fishery.

I have left out institutional barriers since this is a people problem, and I left out prices because that is a marketing problem.

We also have three ways we can apply technology to reduce operating costs. We can do this by cutting the crew size by mechanization; by cutting the search time with sonar, and forecasting and fish scouting services; and by developing low-cost vessels designed specifically for this fishery and the weather conditions we have off the California coast.

I have not tried to put any dollar values on these proposals mainly because to do so would require more data than I have available. I think you will agree that each and every proposal is open to analysis and it should not take too long to establish an order of priorities for implementation.

7110

SURFACE TUNA-SCHOOL FISHING & BAITING AROUND SAMOA ISLANDS

Thomas S. Hida

The NMFS research vessel 'Charles H. Gilbert' returned to Honolulu on April 14, 1970, after completing a series of offshore and inshore surveys around the Samoa Islands. One of her primary missions was to survey the distribution and abundance of surface tuna schools through visual observations, trolling, and live-bait pole-and-line fishing. In the vicinity of the islands, 144 schools were seen. These included 28 skipjack tuna, 11 yellowfin tuna, and 10 mixed yellowfin-skipjack tuna schools.

Most of the observations and all of the live-bait fishing were carried out during the offshore surveys. Baiting was carried out in conjunction with live-bait pole-and-line fishing.

Other objectives accomplished by the 'Gilbert' included: (1) collecting blood samples from 216 skipjack tuna, Katsuwonus pelamis, and 26 yellowfin tuna, Thunnus albacares, for subpopulation studies; (2) making thirteen 30-minute surface plankton tows with a 1-meter net for larval tuna studies; (3) tagging and releasing 840 skipjack and 91 yellowfin tunas for growth and migration studies, and (4) conducting 35 inshore bottom fishing stations and a few miscellaneous stations in cooperation with the Government of American Samoa.

Because reports dealing with baiting and pole-and-line fishing near Samoa Islands are scarce, the cruise findings regarding these operations are presented in detail. (The results of the four other objectives will be reported elsewhere.)

OFFSHORE SURVEY

Pole-and-Line Fishing

A total of 144 schools was sighted in the area covered by two offshore surveys (fig. 1). In most instances, schools were accompanied by bird flocks composed of a few to over 1,000 birds. Birds most commonly associated with the schools were terns, boobies, and shearwaters. Schools sighted were identified as: 28 skipjack tuna, 11 yellowfin tuna, 10 kawakawa, Euthynnus affinis, 10 mixed yellowfin and skipjack tunas, 1 mixed kawakawa, dolphin, Coryphaena hippurus, and shark (unidentified), and 84 unidentified. The locations of the schools, with dates, are given in table 1. Many schools seen were not investigated because they were too far away, too fast or too small; more schools would have been fished had there been more live bait available. Sixteen schools were successfully fished. The catch included 1,075 skipjack tuna (4 to 17 pounds), 160 yellowfin tuna (2.5 to 60 pounds), and a few other fish. The locations of the tagged tuna releases are indicated with a "T" in figure 1.

Only 12 of the schools sighted were estimated to be large. Information on these schools, estimated to be over 50 tons, is given in table 2. Five were "breezers," six were "boilers," and one, which was loosely schooled over a wide area, was designated as a "jumper" (see Scott,[1] 1969 for school descriptions). Activity of the "boilers" was not intense, with fish breaking surface only in small patches in pursuit of forage. Six of the schools had 5-10 pound skipjack tuna, two schools were of 20-50 pound yellowfin tuna, and four were mixed schools of 5-11 pound skipjack tuna and 5-60 pound yellowfin tuna. Locations of the large schools are indicated in figure 1 with an "X".

Trolling

Surface trolling was conducted with four lines during most of the daylight runs. Identification of schools and size of fish were often determined by troll-caught fish, especially during the second offshore survey when there was a shortage of live bait aboard the

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[1] "Tuna Schooling Terminology," James Michael Scott. Calif. Fish Game 55(2): 136-140. 1969.

COMMERCIAL FISHERIES REVIEW
Reprint No. 896

Table 1.--Noon Positions, Dates and Number and Kinds of Schools Sighted Around the Samoa Islands During Cruise 117 of the 'Charles H. Gilbert'

Noon Position		Date	Number of Schools Sighted[1]						
Lat. (S.)	Long. (W.)	1970	SJ	YF	KK	Mixed YF, SJ	UN	Mixed KK, DO, SK	Total
12°00'	169°15'	2/8	-	-	-	-	4	-	4
South of Pago Pago		2/11	-	-	-	-	5	-	5
16°55'	170°45'	2/12	2	1	-	-	4	-	7
16°03'	170°13'	2/13	4	-	-	-	2	-	6
14°33'	170°23'	2/15	2	-	-	-	2	-	4
14°30'	169°22'	2/16	-	1	-	1	3	-	5
13°37'	169°24'	2/17	-	-	-	-	1	-	1
14°09'	171°00'	2/23	-	-	1	-	2	-	3
14°27'	171°45'	2/25	1	-	-	-	-	-	1
13°49'	173°15'	2/26	-	3	-	2	4	-	9
13°50'	172°08'	2/27	-	-	2	-	3	-	5
14°12'	172°12'	3/1	1	1	1	1	1	-	5
14°45'	171°02'	3/2	1	-	-	-	5	-	6
14°19'	170°36'	3/5	-	-	-	-	3	-	3
14°18'	170°35'	3/6	-	-	-	-	4	-	4
14°19'	170°39'	3/10	-	-	1	-	1	-	2
14°17'	170°53'	3/11	-	-	1	-	-	1	2
14°51'	170°30'	3/14	2	-	-	-	1	-	3
14°11'	170°14'	3/18	-	2	-	-	4	-	6
14°02'	169°22'	3/19	-	-	-	2	4	-	6
14°39'	168°36'	3/20	4	-	-	1	2	-	7
14°38'	170°14'	3/21	3	-	-	-	5	-	8
14°25'	170°47'	3/23	3	-	-	-	4	-	7
15°42'	170°45'	3/24	-	-	-	-	2	-	2
14°23'	170°35'	3/25	-	-	-	-	1	-	1
14°15'	170°56'	3/26	2	1	1	1	4	-	9
13°46'	171°45'	3/27	-	-	-	-	2	-	2
13°42'	173°08'	3/28	1	1	-	-	3	-	5
14°15'	172°29'	3/29	-	-	1	-	5	-	6
13°44'	171°50'	3/31	-	-	2	2	1	-	5
15°03'	171°16'	4/1	2	1	-	-	2	-	5
Total			28	11	10	10	84	1	144

[1] SJ = skipjack; YF = yellowfin; KK = kawakawa; UN = unidentified; DO = dolphin; SK = shark.

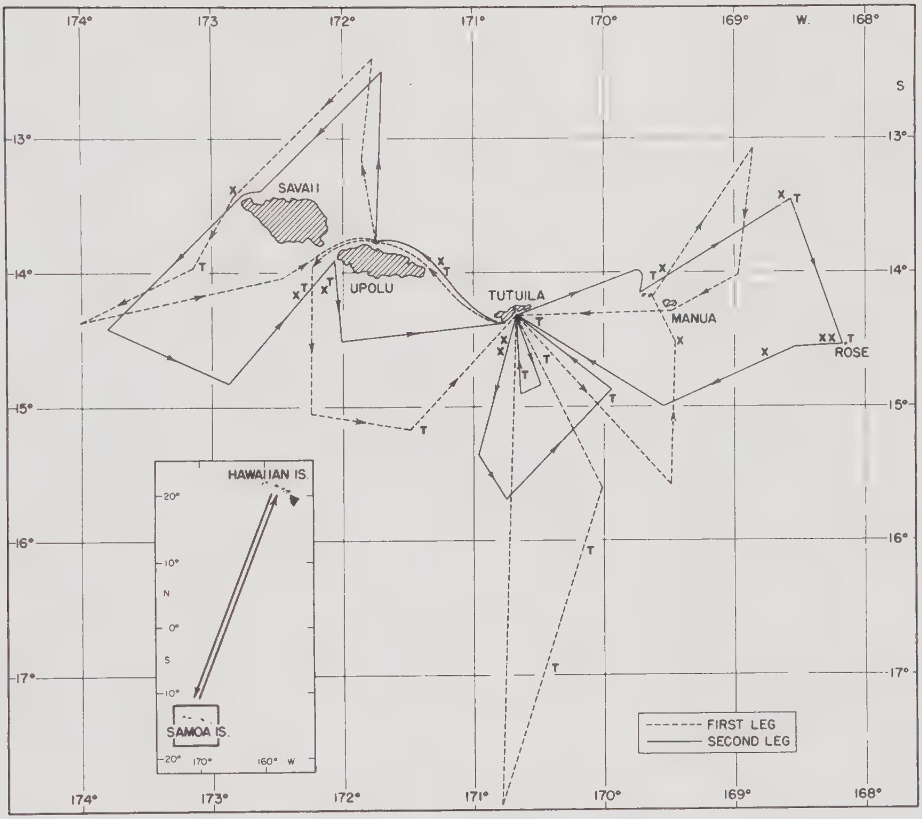


Fig. 1 - Offshore survey track chart, 'Charles H. Gilbert' cruise 117, January 30-April 14, 1970, showing locations of tag releases "T" and large schools "X."

'Gilbert'. The troll catches included 46 skipjack tuna, 30 yellowfin tuna, 31 kawakawa, 2 dolphin, and 1 shortbill spearfish, Tetrapturus angustirostris.

Environmental Conditions

The surface temperatures recorded by expendable and mechanical bathythermographs around the Samoa Islands during the survey ranged between 28° and 30° C. The thermocline depths were usually 30 to 60 meters ranging from 20 to 78 meters. The thermocline was not as "sharp" as that encountered in the Equatorial Countercurrent and the eastern tropical Pacific. Temperatures were typically 25°-27° C. at a depth of 100 meters; 20°-23° C. at 200 meters; and 15°-16° C. at 300 meters. The weather changed rapidly in the area, with seas mostly moderate and winds usually blowing from points between northeast and southeast. The water color was the typical deep blue of the open tropical Pacific.

Transported Bait

Prior to leaving Honolulu, 135 buckets of threadfin shad, Dorosoma petenense, were loaded into three baitwells aboard the 'Gilbert' for use as live bait in pole-and-line fishing. The shad had been acclimated to sea water and were held in swimming pools for several months prior to the cruise. Shad mortalities were high during the rough 10-day voyage to Samoa. Only 30 buckets survived, but these worked well as chum during the first offshore survey for as long as they were available.

Table 2.--Information on Large Tuna Schools Seen in the Vicinity of the Samoa Islands During Cruise 117 of the 'Charles H. Gilbert'

Position		Date	Species	Fish Size	Type of
Lat. (S.)	Long. (W.)	1970	Common Names of Tuna	Pounds	School[1]
14°30'	169°21'	2/16	Yellowfin	20-50	Boiler
13°25'	172°45'	2/26	Yellowfin	30-40	Boiler
14°09'	172°11'	3/1	Yellowfin-Skipjack	7-16	Boiler
14°12'	169°35'	3/19	Yellowfin-Skipjack	5	Breezer
13°30'	168°41'	3/19	Skipjack Yellowfin	11 60	Breezer
14°39'	168°25'	3/20	Skipjack	10	Boiler
14°37'	168°25'	3/20	Skipjack	10	Boiler
14°45'	168°51'	3/20	Skipjack	6	Boiler
14°26'	170°42'	3/23	Skipjack	8	Breezer
14°27'	170°46'	3/23	Skipjack	7-8	Breezer
13°54'	171°21'	3/26	Skipjack	5	Breezer
14°12'	172°04'	3/31	Skipjack Yellowfin	6 9	Jumper

[1] See Scott, 1969 for school terminology.

INSHORE BAIT SURVEY

Tutuila, American Samoa

Bait scouting was conducted from the shore in Tafuna, Alofau, and Fagasa Bays. Baiting conditions were poor in all three localities and suitable baitfish scarce. Therefore, baiting was confined to Pago Pago Harbor. A night light was submerged a few feet below the sea surface whenever possible in Pago Pago Harbor in depths ranging from 13 to 20 fathoms. Only eight sets with a lampara net were made around the light. No set was made unless an accumulation of baitfish was seen under the light.

A total of 54 buckets of a mackerel, Rastrelliger kanagurta, 22 buckets of sardines, Sardinella melanura and Herklotsichthys punctatus, and 4 buckets of bigeye scad, Trachurops crumenophthalmus, was caught night baiting. Small jacks, silversides, mullets, and a few other fish were also caught. Juvenile bigeye scad were not caught in large quantities, although it was the most common fish hooked by natives in the harbor.

Most Rastrelliger and sardines were 5 to 7 inches long and were considered too large to be an effective live bait for small skipjack tuna. Problems were encountered in trying to keep Rastrelliger alive in the baitwells. On two occasions, after a few hours in the baitwells, they began surfacing in convulsive movements, turned on their sides and sank to the bottom. Mortality was very high and believed to be the result of oxygen deficiency. Unlike the other bait species, this larger baitfish could not be crowded into the baitwells.

Thirty-one sets were made with a bait seine (22 feet deep by 80 fathoms long) in 8 days of baiting in Pago Pago Harbor. Eighty-eight buckets of sardines, the most prevalent species, were caught; the largest catch in one set was 20 buckets. A few silversides, juvenile jacks, surmullets, mullets, anchovies, tangs, and puffers were also caught in the seine. A few attempts to set on Rastrelliger during the day in the deeper parts of the harbor were unsuccessful because they swam under and out of the seine before it could be pursed.

In summary, the most common baitfish found in Pago Pago Harbor with possibilities as a live bait was Rastrelliger, followed by sardines. The harbor was deep, mostly over 13 fathoms, and offered fairly good baiting conditions. Day seining for Rastrelliger would probably be more effective using a seine 30-40 feet deep. At the time of the surveys, most Rastrelliger and sardines were larger than desired as chum for small skipjack tuna. It is assumed that they would have been smaller and more suitable as live bait had the survey been conducted a few months earlier. Also, smaller ones may prefer areas other than Pago Pago Harbor and may have eluded detection during this survey.

Upolu, Western Samoa

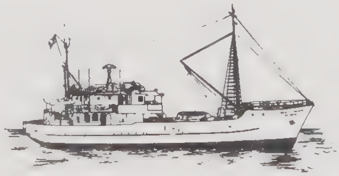
In Western Samoa, bait scouting was limited to Apia Harbor. Little bait was evident around the main dock area and the adjacent shoreline, but the shallower and sandier grounds along the northwestern shores of the harbor appeared more suitable for baiting.

Observations under night lights showed a scarcity of suitable baitfish. Only a few mullet and schools of tigerfish (Theraponidae), which were too large for use as live bait, were attracted to the light. Five daytime seine sets were made in the harbor. The catch included 13 buckets of large (3-4 inch) silverside, tentatively identified as Hepsetia pinguis (Lacepède), and 5 buckets of small (2.5-inch) sardines. The silverside died in the baitwell before they could be used for fishing, probably affected by the long skiff ride from baiting area to vessel. The sardines, on the other hand, did very well in the baitwell and were effective as chum.

Baiting was poor in Apia Harbor during the survey. Further scouting should be conducted in other areas and at different times to better assess the live-bait resources of Western Samoa.

ACKNOWLEDGMENTS

Mr. Peter Whitehead of the British Museum (Natural History) was kind enough to identify the sardines from samples sent to him. Mr. Susumu Kato of NMFS, Fishery-Oceanography Center, La Jolla, Calif., and Mr. Hiromu Heyamoto of NMFS, Exploratory Fishing and Gear Research Base in Seattle, reviewed this paper.



7111

BAITFISH SCOUTING IN THE TRUST TERRRITORY

Thomas S. Hida

The NMFS 'Townsend Cromwell' departed Honolulu for the western Pacific April 9, 1971. She stopped at numerous islands in the Marian, Palau, Caroline, and Marshall Islands before returning to Honolulu on July 8, 1971. One primary mission was to scout for concentrations of baitfish that would be used for live-bait, pole-and-line skipjack-tuna fishing, and purse-seining purposes. Large concentrations of sardines were found on Jaluit and Majuro in the Marshall Islands. Most islands to the west and south of Truk had no substantial amount of baitfish other than the round herring, which was found in fair-to-good quantities. However, Hawaiian skipjack-tuna fishermen have found these to be very weak baitfish which, they claim, live only a few hours in the baitwells.

The primary purpose of cruise 53 of the 'Townsend Cromwell' was to determine the availability and abundance of bait species suitable for surface pole-and-line skipjack-tuna fishing and for purse-seining operations in the Trust Territory of the Pacific Islands. This was the first of three cruises planned for this region.

The Japanese investigated the skipjack resources of Micronesia soon after taking over the islands from Germany at the beginning of World War I (Wilson, in press). They began fishing skipjack tuna commerciallly in Palau from 1925 and, by 1937, had built up a fairly large fishery that reached a peak of 33,000 metric tons. Most of the tuna were landed in Truk and Palau, others in Ponape and Saipan. It was estimated that about 40 skipjack fishing boats operated in Truk before World War II.

Presently, about a dozen Okinawan skipjack-tuna fishing vessels operate out of Koror, Palau. The Palauan skipjack fishery has developed gradually over the past several years. Catches have increased accordingly. It seems that more skipjack tuna can be harvested from Micronesia, and fishery researchers are looking for means to accomplish this.

Cruise 53 included stops at many islands (Fig.). By necessity, the surveys were brief and the two succeeding cruises may alter the conclusions presented here.

PROCEDURE

The surveys were conducted by walking and diving along the shoreline of the islands, scuba diving in the deeper waters, observing while cruising along on small skiffs, and by working night light stations. Two Boston whalers and a Hawaiian-type bait skiff with outboard motors, each with two or more observers, made the surveys. A 300-watt light bulb utilizing ship's power, and a 50- or 150-watt light bulb operated off a gasoline-powered portable generator, were used for night lights. The bulbs were submerged from a few feet to about a fathom. Samples of baitfish were caught by dip net, cast net, day seine, night net, night trap, and spear.

Courtesy calls were made on the chief or spokesman of nearly all of the islands where scouting stops were made. Permission was obtained before any bait survey or sampling was conducted. Most chiefs or spokesmen consented without hesitation. Peace Corps workers were very helpful in interpreting and,

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For itinerary and complete findings of baitfish survey, by islands, write for Reprint No. 925, NOAA Publications, AD 165, Bldg. 52, Connecticut Ave. & Van Ness St., NW., Washington, D.C. 20234.

COMMERCIAL FISHERIES REVIEW
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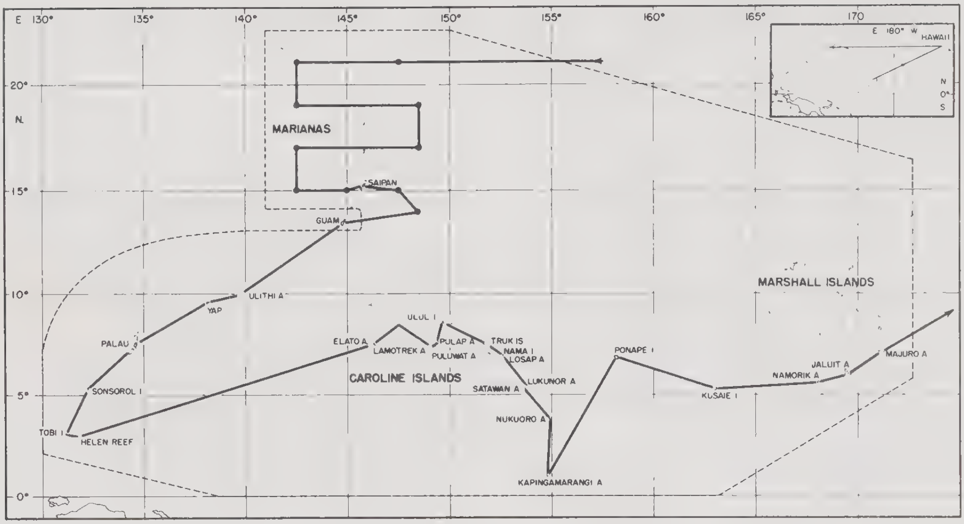
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Track chart of 'Townsend Cromwell,' cruise 53, in the Trust Territory of the Pacific Islands.

at times, were instrumental in persuading chiefs to sanction our work. Most chiefs and elders were able to converse in Japanese, and many interviews were conducted in it.

RESULTS

The baitfish species found at nearly all atolls and islands were:

Goatfish	- mostly Mulloidichthys samoensis
Jack	- mostly Caranx spp.
Round herring	- Spratelloides delicatulus
Cardinalfish	- species of Apogonidae
Bananafish	- species of Caesionidae
Silverside	- species of Atherinidae
Damselfish	- species of Pomacentridae

The round herring were most abundant in the lagoons of large atolls. They were seen while diving along coral outcroppings, or from skiffs when frightened by the approach of the skiffs, or when pursued by predators. Normally, they accumulated under night lights on dark nights. The juvenile goatfish and jacks were common but rarely found in large-enough concentrations to be used as baitfish. They could be seen by walking or diving along the shore, in the shallows or, at times, along the lagoon drop-off.

The cardinalfish could be found at times concentrated in large coral heads. They were also seen scattered along shallow reefs around coral rubble, but so sparsely that it would be impractical to catch them in quantities sufficient for use as baitfish. The bananafish were usually found over coral outcroppings close to the lagoon drop-off. Some schools were estimated to consist of about 10 buckets (a bucket equals 8 pounds). The silverside were usually found close to the shoreline in shallow water. In mangrove areas, they were spread lightly throughout most of the root area, which made them very difficult to catch. The damselfish were usually spread out over coral heads, over coral rubble, in the shallows, and along the lagoon drop-off.

In addition to the baitfish found in the atolls to the west and south of Truk, a few others were found to the eastward:

Anchovy	- Stolephorus heterolobus and S. Indicus
Damselfish	- species of Pomacentridae
Round herring	- Spratelloides delicatulus
Sardine	- Herklotsichthys sp. and possibly Sardinella sp.
Silverside	- species of Atherinidae

The sardines were found in the largest concentrations on Jaluit and Majuro atolls, in shallow areas of less than 3 fathoms. The silverside were also quite abundant in the shallows. Anchovies were found in the deeper parts of the harbor and entrance to Ponape, and also in Kusaie Harbor. Quite a few schools of anchovy were seen in Ponape. But, due to harbor depth (about 40 ft), our 21-ft seine was unable to catch them for estimates of abundance. The damselfish were scattered throughout the lagoon drop-off over coral heads. The round herring were abundant over coral outcroppings and widespread in lagoon areas.

OBSERVATIONS ON TUNA SCHOOLS

There were 122 schools sighted during the cruise. Of these, 92 were unidentified, 21 were skipjack tuna, 5 were yellowfin tuna, 2 were porpoise (Delphinus (?)), 1 was common dolphin (Coryphaena hippurus), and 1 was a mixed school of skipjack and yellowfin tunas. For the area covered during this cruise, the number of schools seen was considered poor. An increase in sightings occurred just to the north and east of Wake, at about lat 21° N. Flocks of migrating shearwaters (Procellariidae) were also seen for a few days while crossing this area. Another increase was noted in the vicinity of Helen Reef and to the northeast at about lat 4° N. Even in these two areas, where a relatively good number of schools was sighted, the prospect for pole and line or purse seining was not favorable. This lack of good fish signs was evident throughout the cruise. The time of the survey was not the season for tuna school abundance in this area (Tohoku Regional Fisheries Research Laboratory, undated).

CONCLUSIONS

The best concentration of baitfish was in the Marshall Islands. A school of sardine estimated to exceed 25 tons was seen at Jaluit; thousands of buckets more of sardine, silverside, and a few other baitfish were seen along the shoreline of the fringing islands. Thousands of buckets of sardine, silverside, and a few other baitfish were also seen along the shoreline on Majuro atoll. Interviews with several people on Majuro also revealed that other atolls in the Marshall Islands carry heavy concentrations of sardine.

Ponape was the only island where a good number of anchovy (Stolephorus heterolobus) schools was seen. They were mostly in the harbor and along the channel but could not be caught with the shallow day seine. The anchovy were in the deeper part of the harbor, where a deep lampara net is needed to catch them. Night lights attracted only a few buckets of them, but this method should be more productive under the right conditions. This same species is caught exclusively by night net in the Palau Islands. Kusaie had a few anchovy, but a good assessment was not obtained because of turbid conditions and time limitations.

I thank the crew, scientific staff, and observers who helped make this cruise possible.

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CLEANING SYMBIOSIS AMONG CALIFORNIA INSHORE FISHES[1]

EDMUND S. HOBSON[2]

ABSTRACT

Cleaning symbiosis among shore fishes was studied during 1968 and 1969 in southern California, with work centered at La Jolla. Three species are habitual cleaners: the señorita, *Oxyjulis californica*; the sharpnose seaperch, *Phanerodon atripes*; and the kelp perch, *Brachyistius frenatus*.

Because of specific differences in habitat, there is little overlap in the cleaning areas of these three species. Except for juvenile sharpnose seaperch, cleaning is of secondary significance to these species, even though it may be of major significance to certain individuals. The tendency to clean varies between individuals. Principal prey of most members of these species are free-living organisms picked from a substrate and from midwater—a mode of feeding that favors adaptations suited to cleaning.

Because it is exceedingly abundant in a variety of habitats, the señorita is the predominant inshore cleaning fish in California. Certain aspects of its cleaning relate to the fact that only a few of the many señoritas present at a given time will clean, and that this activity is not centered around well-defined cleaning stations, as has been reported for certain cleaning fishes elsewhere. Probably because cleaners are difficult to recognize among the many señoritas that do not clean, other fishes generally do not attempt to initiate cleaning; rather, the activity is consistently initiated by the cleaner itself. An infested fish approached by a cleaner generally drifts into an unusual attitude that advertises the temporary existence of the transient cleaning station to other fish in need of service, and these converge on the cleaner. Although señoritas, as a group, clean a number of different fishes, a given individual tends to initiate cleaning with members of just one species.

The fishes cleaned most often are those which are most abundant and, at the same time, are most heavily infested with external parasites. The most numerous ectoparasites are caligid copepods, the most abundant and widespread of which is *Caligus hobsoni*. These particular parasites, along with gnathiid isopod larvae, are the major prey of the cleaning fishes. Cleaning is essentially limited to the external body surface; ectoparasites of the oral and branchial cavities are not ordinarily taken. Cleaning effectively reduces the number of parasites on fishes that are cleaned, and is an important activity for the organisms involved. However, there is no basis for the contention that many good fishing grounds in southern California exist because fishes have congregated in these locations for cleaning.

It has been suggested that many of the better inshore fishing spots are, in fact, cleaning stations (Limbaugh, 1961; Feder, 1966). The contention is that fishes congregate at these locations so that ectoparasites and other deleterious material can be removed from their bodies by resident cleaning organisms. Critics of this hypothesis might well suggest instead that cleaners simply are especially active where fishes are most abundant, or that the cleaners as well as those they clean occur at these locations for reasons that have nothing to do with cleaning. Regardless of which view is correct in a given situation, one having witnessed fishes crowded around a cleaner, vigorously soliciting its services, can only conclude that this activity is indeed important to the organisms involved.

Cleaning symbiosis has been widely described in the literature (Longley and Hildebrand, 1941; Eibl-Eibesfeldt, 1955; Limbaugh, 1955, 1961; Randall, 1958, 1962; and others) and was reviewed by Feder (1966). Youngbluth (1968) studied activity of the Hawaiian cleaning labrid *Labroides phthirophagus* in some detail, and Losey (1971) analyzed the communicative signals between this same species and the fishes that it cleans. But most other reports on cleaning have been simple treatments based largely on

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incidental observations. In this report, I describe cleaning symbiosis among inshore fishes of southern California and attempt to relate observed activity with the incidence of specific ectoparasites.

Conrad Limbaugh, Scripps Institution of Oceanography, was among the first to report cleaning symbiosis among California fishes. In a study of fishes of the kelp beds, Limbaugh (1955) described cleaning by the señorita, *Oxyjulis californica*, a fish of the family Labridae, and also by several seaperches of the family Embiotocidae: the kelp perch, *Brachyistius frenatus;* the black perch, *Embiotoca jacksoni;* and the pile perch, *Rhacochilus vacca.* Subsequent observers have described cleaning by the rainbow seaperch, *Hypsurus caryi* (Gotshall, 1967); the sharpnose seaperch, *Phanerodon atripes* (Clarke, Flechsig, and Grigg, 1967; Gotshall, 1967; Hobson, 1969a); and the blacksmith, *Chromis punctipinnis* (Turner, Ebert, and Given, 1969).

SPECIES STUDIED

Most of the cleaning observed during this study was performed by the señorita (Figure 1), which by virtue of its great abundance in a variety of habitats is the predominant cleaner inshore. The sharpnose seaperch (Figure 2) was frequently observed cleaning, but its activity is centered in deeper water. The kelp perch (Figure 3) may be an important cleaner in the canopy region of the kelp forests, where it concen-

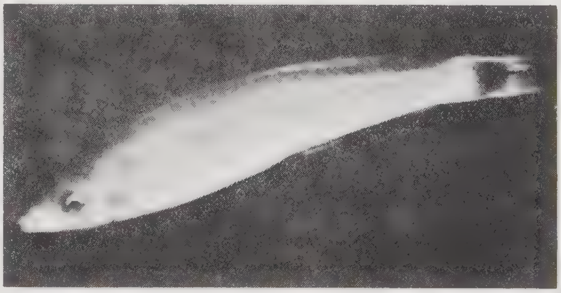

FIGURE 1.—Señorita.

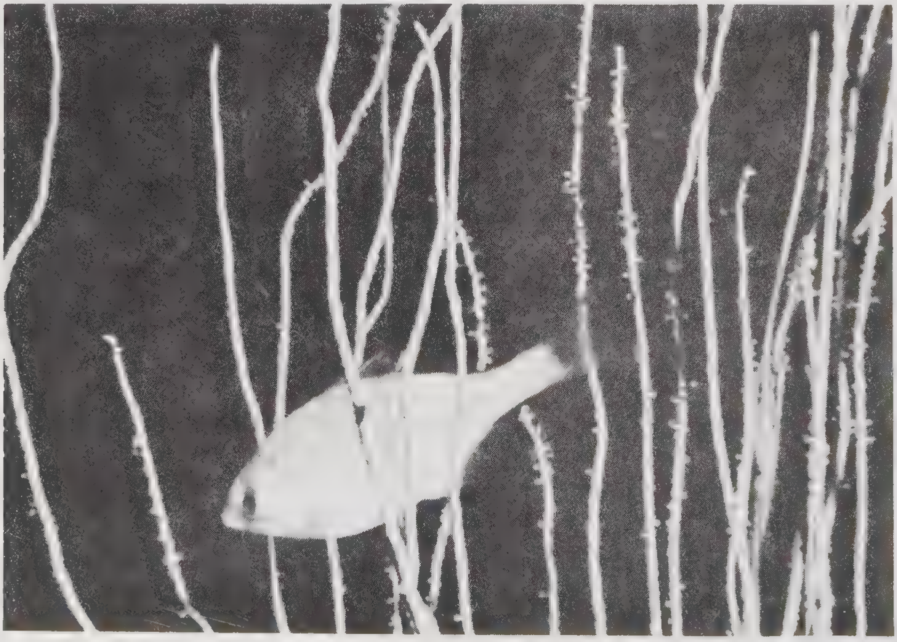

FIGURE 2.—Sharpnose seaperch among branches of a gorgonian.

trates, but this was not determined in this study because observations in the kelp-canopy habitat were infrequent. Nevertheless, observations were sufficient to recognize the kelp perch as a habitual cleaner. The only other fish seen cleaning was the white seaperch, *Phanerodon furcatus,* in which cleaning seemed to be only an occasional incidental activity.

METHODS

During 1968 and 1969, I spent more than 103 hr underwater directly observing cleaning and related activity in California inshore waters. Also contributing to the study are many incidental observations of cleaning made during other work with California fishes between 1961 and 1970.

Supplementing the observations, 421 specimens of 39 species were collected with spear. These represent most of the species common in the study area that exceed a length of 100 mm (all lengths of fishes in this report are standard length). The ectoparasites were collected from all specimens and will be reported in detail elsewhere in collaboration with R. F. Cressey, U.S. National Museum. These collections also provided the material for descriptions of 11 species of copepods formerly new to science (Cressey, 1969a, 1969b, 1970; J. Ho, California State College, Long Beach, unpublished manuscript). Additional undescribed species may occur among a number of copepods from these collections presently under study by Z. Kabata, Biological Station, Nanaimo, British Columbia.

In addition to a survey of the ectoparasites, gut contents of known cleaning species, including material from 53 señoritas, 29 sharpnose seaperch, and 3 kelp perch, were analyzed.

Many ectoparasites leave their host when it is in difficulty, and some fishes regurgitate their stomach contents under stress. To reduce this loss, all specimens were individually sealed in plastic bags immediately upon capture, and while still underwater.

To acquire detailed data on the cleaning interaction, a number of individuals of cleaning species were kept under surveillance for periods

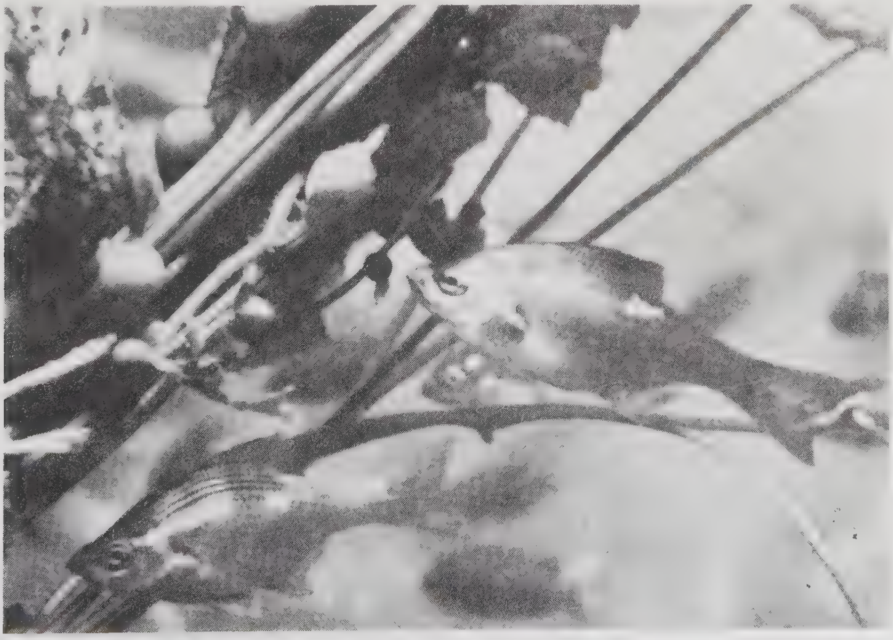

FIGURE 3.—Kelp perch next to giant kelp.

up to 15 min, and a verbal account of their activity was recorded on tape. The attempted standard of 15 min could not be maintained for all these observations because sometimes contact with the fish being watched was lost as the fish swam among vegetation or other fishes. Individuals followed included known cleaners as well as others that had not shown evidence of cleaning. In monitoring the activity of known cleaners, a record was kept of the time during which they showed an apparent cleaning interest in other fish and also the number of cleaning bouts in which they became involved. A cleaning bout is defined here as any cleaning activity involving a discrete group of fishes, whether this group includes one cleaner attending a single fish, or several cleaners attending a cluster of 40 to 50 fish. On various occasions I also recorded the number of times that the cleaner actually "picked" at the body of another fish, and precisely at what point on the body this action was directed.

Study Areas

Observations of cleaning symbiosis were made at many locations throughout southern California, including the Channel Islands, and at the Coronado Islands, Mexico. However, most of the data were collected during concentrated work at La Jolla, Calif. Here, three study sites were established, each including an area of about 100 m^2, that lie on a line running northwest offshore from La Jolla Point. Moving away from the beach along this line, the first station lies in 3 to 10 m of water about 200 m offshore, the second is in 20 to 25 m of water about 700 m offshore, and the third in 30 to 35 m of water about 1000 m offshore. The sea floor at all three stations is rocky and irregular, with many crevices and caves. Algae are not conspicuous at the two deeper stations, which are similar, but the rocks support a heavy growth of gorgonians. On the other hand, the nearshore region of the 3- to 10-m station is richly carpeted with surfgrass, *Phyllospadix*, and other parts of the inshore station are forested by large kelps, particularly giant kelp, *Macrocystis*, and feather-boa kelp, *Egregia*. However, these large kelps are sparse here in comparison to some areas nearby to the south and elsewhere in California. Other details of the principal study area will be introduced as they become pertinent.

During all observation periods at the La Jolla stations a record was kept of water temperatures from surface to bottom, horizontal visibility, and surge conditions.

OBSERVATIONS

GENERAL ECOLOGY

Señorita

The señorita, which attains a length of about 250 mm, is one of the most abundant fishes in the inshore waters of southern California, including the Channel Islands. It occurs from the shoreline to depths exceeding 40 m and is recorded from central California south to central Baja California, Mexico (Roedel, 1953). An inhabitant of water over rocky substrates and among sea weeds, the señorita sometimes swims singly, but more often in groups of from a few to many hundreds of individuals. Like other labrids, it is strictly a diurnal fish, taking shelter under cover at night.

Food habits.—The señorita feeds on a variety of benthic organisms from the surface of both algae and rocks. It also feeds heavily in the midwaters, taking small organisms in the plankton, as well as forms that are attached to or encrusted on drifting algal fragments. All this feeding is accomplished in a characteristic picking manner, a mode of feeding well suited to its pointed snout and the several long, curved canine teeth that project forward at the front of each jaw.

To determine the food habits of this fish in the study area, 26 specimens, 110 to 195 mm long, were speared randomly from the population at large. None of these were cleaning when collected. Food items in their stomachs, ranked as percentage of each item in the entire sample, were as follows: bryozoans encrusted on algae, 43%; caprellid amphipods, 32%; fish eggs, 3%; gammarid amphipods, 2.5%; unidentified crustacean fragments, 4%; and pelecypod mollusks, 2.4%. A number of items each made up less than 1% of the sample, including crab fragments, gastropod mollusks, pycnogonids, and a gnathiid isopod larva. Unidentified material constituted 16% of the sample. The gnathiid larva, a single individual from one señorita, was the only evidence of ectroparasites among this material.

Limbaugh (1955) stated that señoritas are omnivorous carnivores which feed on almost any animal material. Quast (1968) concluded that the principal foods of the señorita are small gastropods and crustaceans associated with algae. Because he found no crabs or pistal shrimps in the diet, Quast suggested that bottom feeding is infrequent; however, having seen señoritas frequently picking on the bottom, I believe there must be some other reason why these prey are not taken more often. Size may be a factor, as crabs and pistal shrimps generally are larger and more heavily shelled than most prey of the señorita.

Movements.—Although individual señoritas may range widely over the bottom in a given locality, they seem to operate within a restricted range. Individual fish, when followed, always criss-cross back and forth within a defined area. Twelve individuals, selected randomly from the population at large and kept under surveillance for 11 to 15 min each, showed no evidence of cleaning.

Señoritas are most abundant at the 3- to 10-m station and become progressively fewer with increasing depth offshore. Nevertheless, even at the 30- to 35-m station the species was among the most numerous present. Fluctuations in numbers were often apparent with changes in water temperature. Some of the movement is vertical. When a layer of colder water moved in over the bottom—a frequent phenomenon at the 20- to 25-m station—señoritas were especially abundant up in the water column above the thermal interface. Seasonal and other longer term changes may induce inshore/offshore movements in certain members of the population. The numbers present fall off noticeably when temperatures drop much below 13° C, but at least some señoritas were present no matter what the conditions. These comments on temperature effects are based entirely on casual evaluations of relative abundance under varying conditions.

Sharpnose Seaperch

The sharpnose seaperch is not regarded as a common species (e.g., Limbaugh, 1955), but was relatively abundant during this study over rocky substrates below 20 m in the La Jolla area. It grows to over 200 mm long and is recorded from Bodega Bay, central California (Miller, Gotshall, and Nitsos, 1965), south to the San Benito Islands, Mexico (Roedel, 1953). Most of those observed during this study were juveniles less than about 125 mm long that swam singly or, more often, in small groups of less than 10 individuals. Adults were seen only occasionally but sometimes swam in larger aggregations. All activity observed in these fish occurred during daylight. After dark they hover above the substrate and are alert, but their activity at this time, if any occurs, was not determined.

Food habits.—This seaperch takes a variety of benthic organisms from the surface of rocks, algae, gorgonians, and other benthic substrates. Prey are taken off the bottom in a characteristic picking manner similar to that of the señorita. However, the seaperch's dentition would seem less specialized for picking than that of the señorita; its conic teeth are relatively short and straight, and those at the front of the jaws are not notably longer than those on the sides, nor do they project forward.

To investigate the food habits of this fish in the study area, 13 individuals, 76 to 170 mm long, were speared randomly from the population at large. None of these were cleaning when collected. Food items in their stomachs, ranked as percentage of each item in the entire sample, were as follows: caprellid amphipods, 56%; chitons, 9%; planktonic copepods, 9%; isopods, 8%; limpets, 2%; pelycypod mollusks, 1%; and sponges, 1%. Unidentified material made up 14% of the sample. There was no evidence of ectroparasites in this material. One individual had fed heavily and exclusively on planktonic copepods, showing that this fish is not limited to benthic prey. I have found no references to food habits of this fish in the literature.

Movements.—On the basis of limited observations, these fish do not seem to move around in their habitat as much as señoritas do. Nevertheless, they do show marked inshore/offshore movements that may relate to changing water temperatures. Unlike the ubiquitous señorita, this fish occurred in limited numbers that allowed assessing relative abundance through actual counts. It was never seen at the 3- to 10-m station but was reasonably abundant (10-20 individuals were counted during 15-min periods) on all visits to the 30- to 35-m station. At the 20- to 25-m station its appearance was irregular and closely followed temperature fluctuations. Generally it was rare or absent at the 20- to 25-m station when bottom temperatures rose much above 13° C, and was present (a maximum of 10 was seen during a 20-min period) when the temperature dropped much below this level. As most of the individuals seen were juveniles, a seasonal factor independent of temperature was probably operating here. Nevertheless, short-term temperature changes over the critical range (approximately 12°-14° C at the 20- to 25-m station) were consistently accompanied by the presence or absence of this fish. I emphasize that these assessments of abundance are relative to the numbers of the species regularly present. The señorita was always more abundant than the seaperch at all stations and under all conditions. Thus whereas the seaperch was considered abundant during a period in which 15 individuals were seen, at no time did I find so few señoritas present at any of the three La Jolla stations.

Kelp Perch

The kelp perch was not abundant in the La Jolla study area, where it was seen only at the inshore station. Its distribution is essentially limited to the kelp beds, which were not well developed in the study area at the time of this work. Nevertheless, it is very numerous in California inshore waters that are heavily forested with kelp. Attaining a maximum length of about 150 mm, the kelp perch is recorded from Vancouver Island, Canada, south to central Baja California, Mexico (Roedel, 1953). The kelp perch occurs near the rocky bottom at the base of giant kelp, as well as adjacent to the rising kelp stipes, but is most abundant just under the kelp canopy, near the water's surface. Typically, this fish occurs in aggregations of a dozen or more, but larger individuals frequently are solitary, especially those near the rocky sea floor. Most of my observations of kelp perch were made outside the La Jolla study area, the majority around the Channel Islands.

Food habits.—This perch feeds in a picking manner, similar to that employed by the señorita and sharpnose seaperch. It preys on a variety of organisms from the surface of the surrounding kelp and also feeds extensively on material suspended in the current. Its pointed snout and small, upturned mouth, together with a number of relatively long, curved canine teeth that project forward at the front of each jaw, are well suited to its mode of feeding. The dentition of this fish is similar to that of the señorita, a fact also noted by Hubbs and Hubbs (1954). I did not sample kelp perch from the population at large for food-habit analysis; all those collected were from known cleaning stations. However, Limbaugh (1955) stated that they feed on small crustaceans, particularly those that occur on giant kelp. Quast (1968), who also reported a predominantly crustacean diet, with a preponderance of amphipods, noted that some mollusks and bryozoans are taken as well.

Movements.—Limited observations indicate that aggregations of kelp perch in the canopy, and close to large rocks, remain relatively stable. Several aggregations that were observed over 2 to 3 months did not change appreciably in location or in numbers of individuals. Data on this point are scanty, however.

At night they hover in the same areas in which they are active in daylight, but their activity at this time, if any occurs, was not determined.

CLEANING ACTIVITY OF THE SEÑORITA

Unlike some other cleaners (see Feder, 1966), señoritas do not establish well-defined stations at which they receive other fishes seeking to be cleaned. Rather, the señoritas, as they move over the local area, approach and clean fishes wherever they encounter them.

Despite their great abundance, only a small segment of the señorita population seems predisposed to clean at a given time. The cleaning habit is not limited to any particular stage in their life history: cleaning señoritas have included some of the smallest individuals seen (< 40 mm) as well as some of the largest (> 225 mm). In cleaning material from the bodies of fishes, señoritas employ the same picking technique they use to take small prey from a rock or algal substrate. This mode of feeding, along with their pointed snout and long, forward-projecting canine teeth, are well suited to the cleaning habit.

Individuals that clean are numerous where there are many resident fishes, especially of certain species (as discussed below), but I found no evidence that residents of other areas come to these locations to have parasites removed. Occasionally a migrating species, such as the California yellowtail, *Seriola dorsalis*, will pause to be cleaned while passing through areas where cleaners are active, but this is not the same as a resident of a particular area habitually swimming elsewhere to be cleaned and then returning to its home ground.

Fishes Cleaned by the Señorita

Casual observation alone show that some fish species are cleaned far more often than others, and that many species do not seem to interact with cleaners at all.

To obtain data on this point, a record was kept of the species seen being cleaned by señoritas during 62 observation periods (15 min to 2 hr long) from June 1968 to January 1969. During this period, 392 cleaning bouts were witnessed, 385 of which involved señoritas cleaning one or more individuals of a single species; in only seven instances were señoritas seen cleaning members of a mixed-species group. The tabulation of species cleaned (Table 1) does not include the mixed-species groups because in the mixed groups it was not determined whether representatives of all species present were actually cleaned. All seven mixed groups included halfmoons, *Medialuna californiensis*, and one or more fish of other species. In four of these, halfmoons were mixed with blacksmiths, in one they were mixed with opaleyes (*Girella nigricans*), in one with rubberlip perch (*Rhacochilus toxotes*), and in one with both rubberlip perch and pile perch. All of these were incidental observations. The compilation does not include data obtained on other occasions when the activity of individual cleaners was recorded for extended periods.

The data clearly indicate that blacksmiths, and to a lesser extent topsmelt (*Atherinops affinis*), predominate as recipients of the señorita's cleaning efforts in the areas where the observations were made. Table 1 is not a definitive list of species cleaned by the señorita; nevertheless, it is evident that many species which co-occur with the señorita are not cleaned. At other times, in addition to all species noted in Table 1, I have seen *Seriola dorsalis* and *Trachurus symmetricus* being cleaned. But the ratio of species listed here generally is consistent with observations made on other occasions and at many different locations.

TABLE 1.—Fishes observed being cleaned by señoritas during 62 observation periods between June 1968 and January 1969 at La Jolla, Calif. (exclusive of seven mixed-species groups).

Species	Number of cleaning bouts	Percent of total bouts observed
Blacksmith, *Chromis punctipinnis*	231	60
Topsmelt, *Atherinops affinis*	81	21
Garibaldi, *Hypsypops rubicunda*	22	6
Halfmoon, *Medialuna californiensis*	19	5
Señorita, *Oxyjulis californica*	10	3
Rubberlip perch, *Rhacochilus toxotes*	8	2
Opaleye, *Girella nigricans*	5	1
Kelpfish, *Heterostichus rostratus*	3	1
Black perch, *Embiotoca jacksoni*	1	1
Pile perch, *Rhacochilus vacca*	1	1
Sargo, *Anisotremus davidsoni*	1	1
Blue rockfish, *Sebastes mystinus*	1	1
Olive rockfish, *Sebastes serranoides*	1	1

Reports in the literature present a comparable picture. Most published accounts of cleaning by señoritas describe the way blacksmiths cluster around this cleaner to solicit its attentions (Limbaugh, 1955, 1961; Feder, 1966; and others). Limbaugh (1955) observed the following fish being cleaned by señoritas: *Myliobatis californica, Stereolepis gigas, Paralabrax clathratus, Trachurus symmetricus, Atherinops affinis, Anisotremus davidsoni, Hyperprosopon argenteum, Rhacochilus vacca, Chromis punctipinnis, Hypsypops rubicunda, Girella nigricans, Medialuna californiensis,* and *Mola mola.* Turner et al. (1969) observed the following fish being cleaned by señoritas: *Sebastes* spp., *Atherinops affinis, Atherinopsis californiensis, Trachurus symmetricus, Seriola dorsalis, Chromis punctipinnis,* and *Mola mola.* Neither of these reports gives data on the relative frequency with which these different species were cleaned, but it is significant that many of the same species consistently appear in the reports of independent observers, while at the same time many other species that frequent these waters in large numbers are not mentioned. No doubt many species not yet reported are occasionally cleaned by señoritas, but there seems little doubt that a certain few species, the blacksmith in particular, predominate in this activity.

Specific Cleaning Interactions

The fishes cleaned by the señorita vary markedly in their habits and habitat, as well as in their relative numbers. These fishes do not seek out cleaning at a "station" established by the señorita, but rather receive the señorita on their own grounds during the course of their regular activity. Cleaning interactions often proceed differently with one of these species than with another. Some of these variations in cleaning activity are characterized below.

Señorita-blacksmith interactions.—The blacksmith is one of the most abundant fish over rocky substrates in California inshore waters, where it swims in large stationary aggregations in midwater. It feeds largely on zooplankton (Quast, 1968) and attains a length of about 250 mm.

Generally the first sign of an interaction occurs when a señorita swims up alongside a blacksmith in midwater and closely inspects its body. The blacksmith may then immediately stop swimming and, holding its fins motionless and erect, drift into an awkward-appearing posture. Usually the blacksmith is head-down, but sometimes turns on its sides or is tail-down. On some occasions the blacksmith presents a particular part of its body to the inspecting señorita. The señorita swims about this fish, usually pausing briefly to pick at its body. Immediately following the first sign of this activity other blacksmiths converge on the spot, so that very quickly 10 or more crowd around the cleaner (Figure 4). The señorita soon leaves the original blacksmith and may then move on to one of the others. It may also swim slowly away, whereupon the group of blacksmiths follows along, each attempting to position itself in the señorita's path. Although the señorita shows progressively less interest in the blacksmiths, they continue to crowd in its way. Soon the señorita shows no further interest in cleaning, and all but a few blacksmiths leave the group. The remaining few doggedly continue attempting to present themselves to the now-unresponsive cleaner. Eventually, however, these last blacksmiths lose contact with the cleaner as it swims off among the kelp or the many other señoritas in the surrounding water. Once they have lost contact with the cleaner the blacksmiths do not attempt to solicit cleaning from any of the many other señoritas around them.

On only two occasions did I note blacksmiths soliciting cleaning from a señorita that did not seem to have made an initiating gesture. Once the blacksmiths were very small, about 40 mm long, and in the other observation, at a depth of 27 m, little cleaning had been seen and relatively few señoritas were present. However, in both instances the señoritas were known by me on the basis of earlier observations to be individuals that clean. It is possible that the fishes soliciting attention recognized these señoritas as cleaners through some cue not noted by me. Sometimes when a señorita incidentally passes close to a blacksmith, the blacksmith noticeably pauses in its swimming and looks as

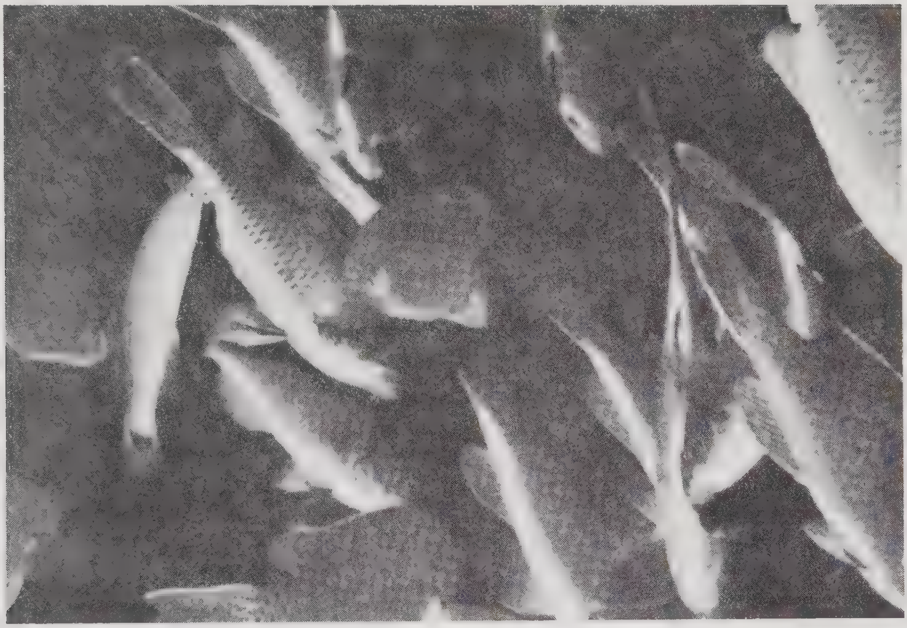

FIGURE 4.—Señorita cleaning the caudal peduncle of one of a group of blacksmiths that hover to solicit service.

though it is beginning to assume a soliciting posture; however, when the señorita swims on past, the blacksmith immediately resumes its original activity. Occasionally members of other species were seen responding similarly to passing señoritas. In most observations of cleaning, my attention was drawn to activity already in progress, so that it was not possible to determine whether cleaner or client had initiated the activity.

Individual señoritas that cleaned blacksmiths during many short-term observations were not seen cleaning any other species. This same situation held true for three individuals, known to have been cleaning blacksmiths, whose activity was monitored in detail on tape for 15 min. When observed for extended periods, señoritas were found to become involved in a succession of separate cleaning bouts. This activity was not restricted to one location but continued at various points over a relatively wide area. Periodically they joined cleaning already underway, or initiated cleaning themselves at a number of different locations—always with blacksmiths. I have no explanation for the fact that a señorita which becomes unresponsive and leaves one group of blacksmiths that still vigorously solicits its service may soon initiate activity again with another blacksmith.

The three individuals whose cleaning activity was monitored for 15 min joined in a mean of 4 separate bouts (range 2-6). For a mean of 11 min of this time (range 6.75-13.25 min) they showed an apparent cleaning interest in blacksmiths, or were accompanied by blacksmiths with which they had earlier initiated a cleaning interaction. When not thus engaged with blacksmiths, they swam in midwater showing no apparent interest in the fishes around them but occasionally picked at drifting scraps of debris, usually algal fragments. During much of the time that they swam in consort with blacksmiths, they closely inspected these fish and actually picked at their bodies a mean of 26 times (range 14-33). Of these picks, 27% were made at the base of the blacksmith's anal fin, 25% on the caudal peduncle or caudal fin, 22% at the base of the pectoral fin, 10% somewhere on the body exclusive of a fin-base or head, 8% on the head, 5% at the base of the pelvic fins, and 3% at the base of the dorsal fin.

Clearly, the bases of the fins receive most of the attention from the señoritas. These data are consistent with the many more general observations made on other occasions. At no time during this study were señoritas seen to clean within the oral or branchial cavities of blacksmiths: all cleaning was directed at the body surface.

Señorita-topsmelt interactions.—The topsmelt, which attains a length of about 200 mm, is abundant in many inshore regions of California coastal waters, but its distribution is more spotty than that of the ubiquitous blacksmith. Like the blacksmith, it feeds largely on zooplankton, which it takes while swimming in large schools at the water's surface. Quast (1968) noted the similarity in diet between topsmelt and blacksmiths, and while acknowledging that their feeding areas may overlap, he pointed out that topsmelt normally swim higher in the water column.

In the La Jolla study area, topsmelt are concentrated at the inshore station over extensive fields of surfgrass that grow in 3 to 5 m of water. They are never far from the substrate in this relatively shallow water, even though they swim in large schools at the water's surface. They are more abundant than blacksmiths in this area, and here they predominate in the señorita's cleaning activity.

The cleaning interaction proceeds in much the same way as it does with blacksmiths: the activity is initiated when a señorita swims up to an individual topsmelt and begins to inspect it closely. Immediately other topsmelt converge on this pair to place themselves in the señorita's path, thus soliciting its attention. When presenting themselves motionless before señoritas, topsmelt frequently hover tail-down, in contrast to the head-down posture most often assumed by blacksmiths. I saw señoritas clean only the external body surfaces of topsmelt. In the relatively shallow water where most of this activity was observed, señoritas break off contact with a group of topsmelt more readily than they do with blacksmiths, as they need only swim down to the substrate below, where the topsmelt seem reluctant to follow.

These shallow areas are frequently swept by surge, and the load of drifting debris in midwater is frequently heavy. In this area cleaning señoritas frequently leave the groups of topsmelt they are attending to inspect an object drifting in the water nearby. Sometimes they take the object into their mouths, sometimes not. Often when taken it is quickly rejected.

Attempts at extended observations on individual señoritas that had been cleaning topsmelt were largely unsuccessful. Too often before the observation had progressed far the señoritas disappeared among the surfgrass or other vegetation carpeting the sea floor in this area. However, two individuals were followed for 10 min each, during which time one entered into four, the other two, separate cleaning bouts. Between cleaning bouts these two swam over a wide area alone in midwater, occasionally picking at drifting debris. On several occasions they picked at benthic algae. Neither individual showed cleaning interest in species other than topsmelt, which was consistent with observations of other señoritas that cleaned topsmelt.

Señorita-garibaldi interactions.—The garibaldi, which attains a length of about 250 mm, is a solitary, highly territorial fish that lives close to the substrate. Especially during the reproductive season, when the males aggressively guard their nests among the rocks, these bright orange pomacentrids normally drive away all other fish that come near. They feed on sessile benthic invertebrates and are abundant at the 3- to 10-m station.

Garibaldis frequently are cleaned by señoritas. Most of the garibaldis seen being cleaned were swimming a meter or so above the bottom; I did not observe cleaners active around the garibaldis guarding nests among the rocks. All of the garibaldis seen being cleaned were solitary, which reflects their territorial nature. The señorita swims up to a garibaldi and closely inspects its body, thus initiating the action. Usually the garibaldi hovers motionless in a normal horizontal attitude, its fins sometimes erect. The señorita may pick at a few places on the garibaldi's body—most often around the caudal region—but usually its attentions are brief, and soon it swims away. With blacksmiths and topsmelt, each cleaning bout is prolonged by the many other individuals that join at the cleaning site to crowd in the señorita's path. Nothing of this sort happens with the solitary garibaldi, which usually makes no attempt to follow the señorita when it leaves, so that each cleaning bout is relatively brief. After leaving one garibaldi, however, often the señorita quickly approaches another. In agreement with their cleaning of blacksmiths and topsmelt, señoritas known to have cleaned garibaldis were subsequently seen cleaning only other members of that same species. This was true during several short-term observations, and also when one individual was followed for 15 min, and a record of its activity was taped; this particular señorita initiated cleaning activity with 26 different garibaldis during the observation period as it swam over an irregular course among the rocks in an area where blacksmiths, topsmelt, and other species also were present. Each cleaning bout lasted a mean of 10 sec (range 7-25 sec), totaling 4 min 15 sec of the 15-min period. In nine of these bouts, the señorita inspected the garibaldi but did not pick at its body. In the other 17 bouts, the señorita picked at the garibaldi's body a total of 42 times, or a mean of about 2.5 times per bout.

All cleaning of garibaldi that I observed was directed at the external body surface.

Señorita-halfmoon interactions.—Halfmoons, which may exceed a length of 250 mm, usually swim high in the water column, frequently in large aggregations, but just as often in small groups or as solitary individuals. They are often abundant among rising stands of giant kelp. Their omnivorous diet, which includes a variety of benthic algae, along with bryozoans, sponges, and crustaceans (Limbaugh, 1955; Quast, 1968), indicates bottom feeding; however, much of this material is taken in midwater as drifting debris.

Considering their large numbers in many southern California coastal areas, halfmoons are not particularly abundant in the principal study areas. Still, they were frequently seen being cleaned by señoritas during this study. When many halfmoons were present, cleaning by the señorita progressed much as described above for blacksmiths. Yet when just one halfmoon was present, a frequent occurrence, the cleaning bouts were brief like those described above for the garibaldi. At least one halfmoon was present in all the mixed-species groups that I recorded when collecting the data presented in Table 1. I saw señoritas clean only the external body surface of halfmoons.

One señorita, seen cleaning a halfmoon, was kept under surveillance for 12 min before contact was lost. As the observation period began, the señorita picked at the halfmoon once and then moved away, swimming slowly and alone, 2 or 3 m over the substrate. After an uneventful 3 min, the señorita approached a second halfmoon, which promptly hovered in a head-down attitude. For 15 sec the señorita closely inspected this halfmoon and picked at its body three times before swimming away. It then continued on alone for the remaining 8+ min that it was under observation, still swimming slowly over a wide semicircular course 2 or 3 m above the rocks. During this time it passed many different fish without showing interest, but it did not pass another halfmoon. It did pick at three different pieces of floating debris but rejected all three immediately.

Señorita-señorita interactions.—Señoritas themselves are cleaned by other members of their own species. Despite the large numbers of señoritas that usually are present, I saw no groups converging on cleaning individuals, as regularly occurs with blacksmiths, topsmelt, and other abundant species. In most of the señorita's intraspecific cleaning interactions, the cleaner attends just a single individual, which usually hovers motionless in a normal horizontal attitude, except that its fins are erected; sometimes the mouth is open wide and gill covers are distended, but I saw señoritas clean only the external body surface of these fish. There was no indication that señoritas which clean other señoritas also clean other species. I followed one individual for 10 min after having seen it clean another señorita. After this initial activity, the individual under surveillance swam over a wide area, showing interest only in other señoritas, even though blacksmiths, topsmelt, and other species were present. Swimming alone, 2 or 3 m over the rocks, it would assume a position alongside another señorita and follow it for a short distance. Usually these other fish showed no interest, but some stopped swimming and erected their fins, whereupon the cleaner picked at their bodies—usually once, but occasionally several times. Between cleaning encounters this señorita passed through a school of very small (< 40 mm) blacksmiths, several of which hovered head-down in its path; however, the cleaner showed no interest in these fish. On two occasions it picked at a piece of drifting debris.

Señorita-kelpfish interactions.—At least one species regularly initiates cleaning bouts with señoritas. Earlier (Hobson, 1965a) I reported observing a kelpfish, *Heterostichus rostratus*, repeatedly soliciting cleaning from unresponsive señoritas. The kelpfish was concealed among benthic algae, which is the typical habitat of this fish. But each time a señorita approached in the water overhead, the kelpfish rose up into the señorita's path, where it hovered motionless, fins erect (Figure 5). A succession of señoritas passed by without responding to the kelpfish, and each time the kelpfish returned to the cover below, where it waited until the next approach. Finally a passing señorita paused briefly and picked at the kelpfish's side before continuing on its way. After this brief encounter, the kelpfish did not rise from concealment again even though several more señoritas subsequently passed overhead.

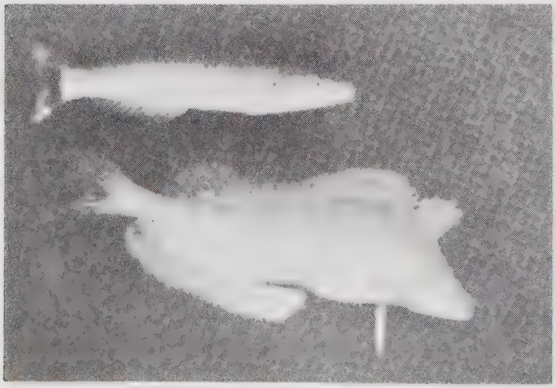

FIGURE 5.—Kelpfish hovering in midwater, fins erect, to solicit cleaning from a passing señorita.

During the present study this sequence of events involving kelpfish and señoritas was witnessed several times at a variety of locations; indeed, every instance of a kelpfish being cleaned followed this pattern—obviously it is a regular pattern in the behavior of the species.

Other interactions—Observations are too few to recognize distinctive aspects in cleaning interactions involving the many other species that occasionally are cleaned by señoritas. Usually such activity is noted simply as occasional sightings of small clusters of fish, or individual fish, hovering before a señorita. In all such encounters, however, only the external body surface was cleaned.

Notes follow regarding two other species that are cleaned by señoritas.

A single señorita was observed cleaning a pile perch, after which its activity was noted for 15 min. Pile perch are not abundant where these observations were made, and after leaving the first individual, the señorita swam alone in midwater for 14 min. It moved over a wide semicircular course during this time and showed no interest in any of the many fish that it passed, although none were pile perch. It did pick at three small items drifting in midwater. After 14 min it made an abrupt course change and, with slightly accelerated swimming, went directly to a solitary pile perch that was in midwater about 10 m away. The señorita swam about the pile perch, which now hovered head-down, but after a close inspection lasting about 10 sec it moved on without picking at the pile perch's body.

Many of the fishes cleaned by señoritas occasionally start, as if nipped too vigorously. Sometimes such fish dart away, thus terminating the cleaning. Other times they actively turn on the señorita and drive it away. The rubberlip perch was noted taking the latter course of action perhaps more often than the other species, even considering the relatively few times it was observed being cleaned.

Although the kelpfish is the only species that was observed consistently initiating cleaning from señoritas, individuals of several species do so in at least one situation. This occurs where exceptionally large concentrations of señoritas, sometimes thousands, swim above the rocks. At various times, garibaldis, pile perch, rubberlip perch, olive rockfish, and others were observed hovering in the soliciting posture amid these concentrations (Figure 6) until one of the señoritas approached and cleaned them.

Material Removed from Other Fishes by the Señorita

Food habits of cleaning señoritas.—An obvious question is: What do señoritas remove from the bodies of fishes they clean? Limbaugh (1955) stated that señoritas remove bacteria, parasitic copepods, and isopods. He was not more specific than this, nor did he present data. Various other cleaners reportedly take not only ectoparasites but also diseased and necrotic tissue (Feder, 1966, and others.)

To determine just what it is that señoritas remove from the bodies of other fishes, I examined the gut contents of 27 specimens, 111 to 175 mm long, that were speared while they were cleaning other fishes. Food items in their guts, ranked as percentage of each item in the entire sample, were as follows: caligid copepods, 39%; gnathiid isopod larvae, 12%; algae with encrusting bryozoans, 10%; caprellid amphipods, 5%; fish scales, 4%; and fragments of nonparasitic crustaceans, 4%. Unidentified material made up 26% of the sample. Of the 27 specimens, ectoparasites occurred among the gut contents of all but two. In most, the ectoparasites predominated. Even though the data are convincing, they do not fully reflect the extent to which cleaning obviously dominated the activity of these particular fish for at least several hours leading up to their capture. This is because the

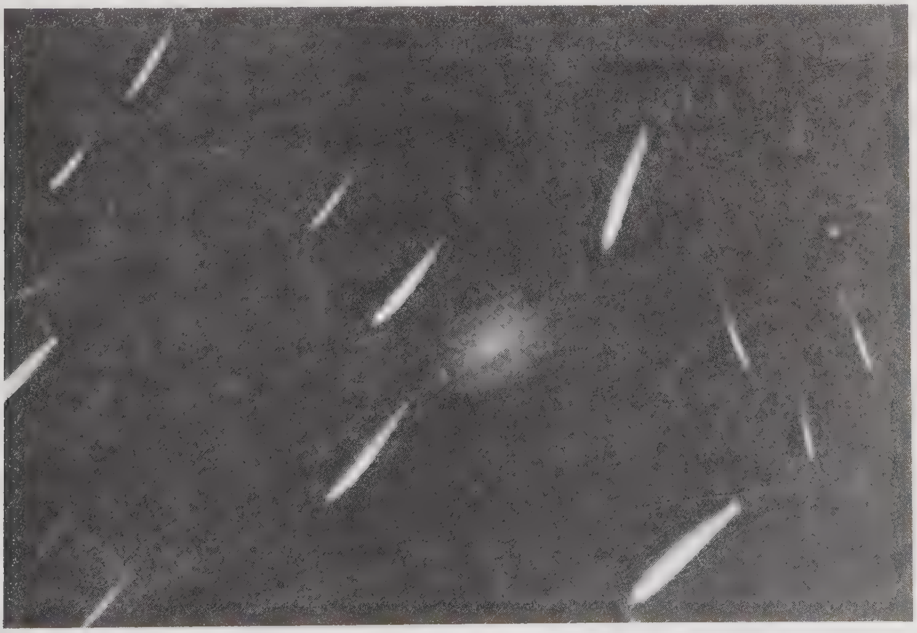

Figure 6.—Garibaldi hovering amid a large assemblage of señoritas.

parasites are so small (1-3 mm long) in comparison with the size of other food items. For example, 471 gnathiid isopod larvae were present in one señorita gut, but being so small they constituted only 35% of the material. On the other hand, a few algal fragments, with encrusting bryozoans, made up 40% of the material in this same specimen. However, only seven individuals contained ectoparasites alone, as compared with 17 that contained both parasites and free-living prey. In all but one of these, the two classes of material were sharply divided in the gut, usually with the free-living material posteriorly in a more advanced stage of digestion. Although most of the ectoparasites in the gut had undergone extensive damage and would not, by themselves, have been identifiable to species, this material usually graded gradually to freshly ingested specimens that were readily identified. This fact, coupled with the circumstance that individual señoritas tend to stay pretty much with a single type of food organism during a given period, greatly aided the task of analyzing this material.

Ectoparasites on the fishes.—To assess the significance of cleaning in removing ectoparasites, one must know what parasites occur on the fishes, as well as the extent of the infestation. Thus the survey of ectoparasites done in conjunction with this work included essentially every fish species exceeding 100 mm long regularly present in the La Jolla study area, as well as every species that was seen being cleaned there. Ectoparasites infesting these fishes include 33 species of copepods, one species of brachiuran, two species of isopods, one species of leech, and one species of monogenetic trematode. Following is a brief summary of the information being compiled on these parasites in collaboration with R. F. Cressey.

Copepods are the predominant ectoparasites on fishes in this area. The 33 species represent seven families: Bomolochidae (6 species), Caligidae (13 species), Dichelesthiidae (2 species), Lernaeidae (1 species), Chondracanthidae (5 species), and Lerneopodidae (6 species). The one species of the closely related brachiurans is a member of the family Argulidae. The bomolochids, which were found on 12 species of the fishes sampled, are mobile forms about 2 mm long (all lengths of parasites here and below do not include egg cases) that occurred mostly on the gills of their hosts. The caligids, which infested 29 species of the fishes, are mobile forms, 2 to 4 mm long, that occurred mostly on the external body surface of their hosts, although two species were found only in the oral cavity. The dichelesthiids are highly modified forms about 2 mm long that were attached to the gills of two species. The lernaeid is a highly modified form about 5 mm long that was attached to the fins of 12 species. The chondracanthids, which infested five species, are highly modified forms, 3 or 4 mm long, that lived attached in the branchial chamber, including the gills, of their hosts. The lerneopodids, infesting eight of the fish species, are highly modified forms, 2 to 5 mm long, mostly living attached in the branchial and oral cavities, although one individual fish carried several attached to its dorsal fin. Finally, the argulid is a mobile form about 2 mm long that was found on the outer body surface of one species of fish. The fish species hosting representatives of the different copepod and brachiuran families are listed in Table 2, and examples of the six copepod families are illustrated in Figure 7.

Thus a variety of ectoparasitic copepods occur on the fishes, but only caligids were found among the gut contents of the cleaners. Furthermore, although 13 species of caligids (five species of the genus *Caligus* and eight species of the genus *Lepeophtheirus*) occur on fishes in this area, only a relatively few of these are significant as prey of the cleaners, as noted below.

Of the two isopods, one, *Livoneca vulgaris*, a large parasite, about 20 mm long, was found in the branchial chamber of just one species of fish and was not found to be prey of the cleaners. On the other hand, the highly mobile gnathiid larvae (Figure 8), which are about 2 mm long, are a major prey of the cleaners. Only one form of gnathiid was readily recognized, but more than one species may occur among this material. Parasites of the body surface of fishes, the gnathiid larvae were taken on 11 of the fish species sampled, but I suspect that they are actually more widespread and abundant than these data

TABLE 2.—The types of ectoparasites and the fishes they infest, based on a survey of the fishes in the study area. Where more than one species of parasites is included under a heading, the number in parentheses following the name of each fish thereunder indicates how many different species of that type are represented on that fish. For all fish species listed, the number of infested individuals is shown over the number of individuals examined, followed by the range in numbers of individual parasites of that type which were taken from that species of fish.

COPEPODS
BOMOLOCHIDAE (6 species of 3 genera)
Fishes infested with members of this family:
Paralabrax clathratus (1) 2/8: 1-2
P. nebulifer (2) 5/11: 1-20
Phanerodon atripes (1) 1/13: 1
Rhacochilus vacca (1) 3/15: 1
Micrometrus minimus (1) 1/7: 1
Hypsypops rubicunda (1) 1/20: 1
Scorpaena guttata (1) 6/14: 2-56
Sebastes mystinus (1) 1/9: 1
S. serranoides (1) 2/11: 1-8
Oxylebius pictus (1) 1/8: 1
Atherinops affinis (1) 2/13: 1-4
Pleuronichthys coenosus (1) 6/10: 1-11

CALIGIDAE (13 species of 2 genera)
Fishes infested with members of this family:
Paralabrax clathratus (2) 4/8: 1-5
P. nebulifer (3) 4/11: 5-27
Caulolatilus princeps (1) 1/4: 2
Anisotremus davidsoni (1) 1/8: 1
Cheilotrema saturnum (1) 2/16: 1
Medialuna californiensis (2) 12/13: 1-75
Girella nigricans (3) 1/10: 1-14
Embiotoca jacksoni (2) 2/15: 1-2
Phanerodon atripes (1) 5/13: 1-5
Rhacochilus toxotes (3) 10/10: 1-10
R. vacca (2) 4/15: 1-11
Chromis punctipinnis (1) 10/10: 2-39
Hypsypops rubicunda (2) 19/20: 1-144
Pimelometopon pulchrum (3) 13/14: 1-70
Oxyjulis californica (3) 13/38: 1-59
Scorpaena guttata (1) 7/14: 1-14
Sebastes atrovirens (3) 6/16: 1
S. carnatus (2) 3/11: 1
S. chrysomelas (1) 1/7: 1
S. constellatus (1) 2/2: 1-5
S. miniatus (1) 1/5: 2
S. mystinus (3) 5/9: 1-5
S. paucispinis (1) 3/3: 1
S. serranoides (3) 8/11: 1-10
S. serriceps (2) 15/15: 1-25
Scorpaenichthys marmoratus (2) 8/10: 1-42
Heterostichus rostratus (1) 2/13: 1-2

COPEPODS—Cont.
CALIGIDAE—Cont.
Atherinops affinis (1) 13/13: 1-23
Pleuronichthys coenosus (1) 5/10: 1-5

DICHELESTHIIDAE (2 species of 1 genus)
Fishes infested with parasites of this family:
Gymnothorax mordax (1) 1/1: 9
Paralabrax nebulifer (1) 5/11: 2-70

LERNAEIDAE (1 species)
Fishes infested by this parasite:
Trachurus symmetricus (1) 1/7: 1
Anisotremus davidsoni (1) 1/8: 1
Cheilotrema saturnum (1) 2/16: 1-2
Medialuna californiensis (1) 5/13: 2-7
Brachyistius frenatus (1) 1/5: 1
Embiotoca jacksoni (1) 2/15: 1-2
Hypsurus caryi (1) 2/11: 1-2
Phanerodon furcatus (1) 3/12: 1-3
Rhacochilus toxotes (1) 1/10: 1
R. vacca (1) 2/15: 1
Micrometrus minimus (1) 5/7: 1-6
Atherinops affinis (1) 2/13: 1-4

CHONDRACANTHIDAE (5 species of 5 genera)
Fishes infested with parasites of this family:
Oxyjulis californica (1) 13/38: 1-4
Scorpaena guttata (1) 2/14: 1-5
Scorpaenichthys marmoratus (1) 4/10: 1-4
Heterostichus rostratus (1) 7/13: 1-7
Pleuronichthys coenosus (1) 7/10: 1-47

LERNEOPODIDAE (6 species of 4 genera)
Fishes infested by parasites of this family:
Cheilotrema saturnum (1) 1/16: 1
Girella nigricans (1) 1/10: 1
Phanerodon atripes (1) 5/13: 1-4
Rhacochilus vacca (1) 1/15: 1
Chromis punctipinnis (1) 1/10: 1
Sebastes atrovirens (1) 1/16: 4
S. constellatus (1) 1/2: 1
S. miniatus (1) 5/5: 2-8
ARGULIDAE (1 species)
Fish infested with this parasite:
Atherinopsis californiensis 1/1: 2

ISOPODS
CYMOTHOIDAE (1 species)
Fish infested with this parasite:
Sebastes mystinus 1/9: 1

GNATHIID LARVAE (number of species not determined)
Fishes infested with these parasites:
Chromis punctipinnis 1/10: 1
Hypsypops rubicunda 4/20: 1-8
Pimelometopon pulchrum 3/14: 1-4
Sebastes atrovirens 4/16: 1-20
S. carnatus 3/11: 1
S. chrysomelas 1/11: 2
S. constellatus 1/2: 1
S. serranoides 1/11: 1
S. serriceps 3/15: 1-5
Oxylebius pictus 3/8: 1-3
Scorpaenichthys marmoratus 3/10: 2-5

MONOGENETIC TREMATODE (1 species)
Fishes infested with this parasite:
Medialuna californiensis 6/13: 2-16
Girella nigricans 4/10: 1-4
Rhacochilus toxotes 2/10: 1
R. vacca 2/15: 1-18
Hypsypops rubicunda 1/20: 1
Pimelometopon pulchrum 10/14: 1-26
Scorpaena guttata 2/14: 5-8
Sebastes atrovirens 7/16: 1
S. constellatus 1/2: 1
S. miniatus 2/5: 1-2
S. serranoides 3/11: 1-26
S. serriceps 2/15: 1-3
Heterostichus rostratus 6/13: 1-7

LEECH (1 species)
Fishes infested with this parasite:
Hypsypops rubicunda 2/20: 1
Sebastes serranoides 1/11: 4
Heterostichus rostratus 2/13: 1-2

FISHES ON WHICH NO PARASITES WERE FOUND:
Xenistius californiensis 0/1
Halichoeres semicinctus 0/10
Coryphopterus nicholsi 0/5

indicate. They are the most mobile of the parasites, and probably many escaped when their host fish was collected. The monogenetic trematode occurred on the outer body surface of 13 species of fishes, and the leech occurred similarly on 3 species. However, neither was found to be taken by the cleaners. The fish species hosting the various isopods and also the trematode and leech are listed in Table 2. Listed also are the three fish-species on which no ectoparasites were found.

The above summary of the survey results gives a general picture of the ectoparasites infesting the fishes that co-occur with the cleaners and might be regarded as a list of the potential prey of the cleaning fishes. The following material considers the parasites that actually are known to be prey.

Ectoparasites in the diet of cleaners relative to ectoparasites on fishes that are cleaned.—Many of the ectoparasites listed above infest

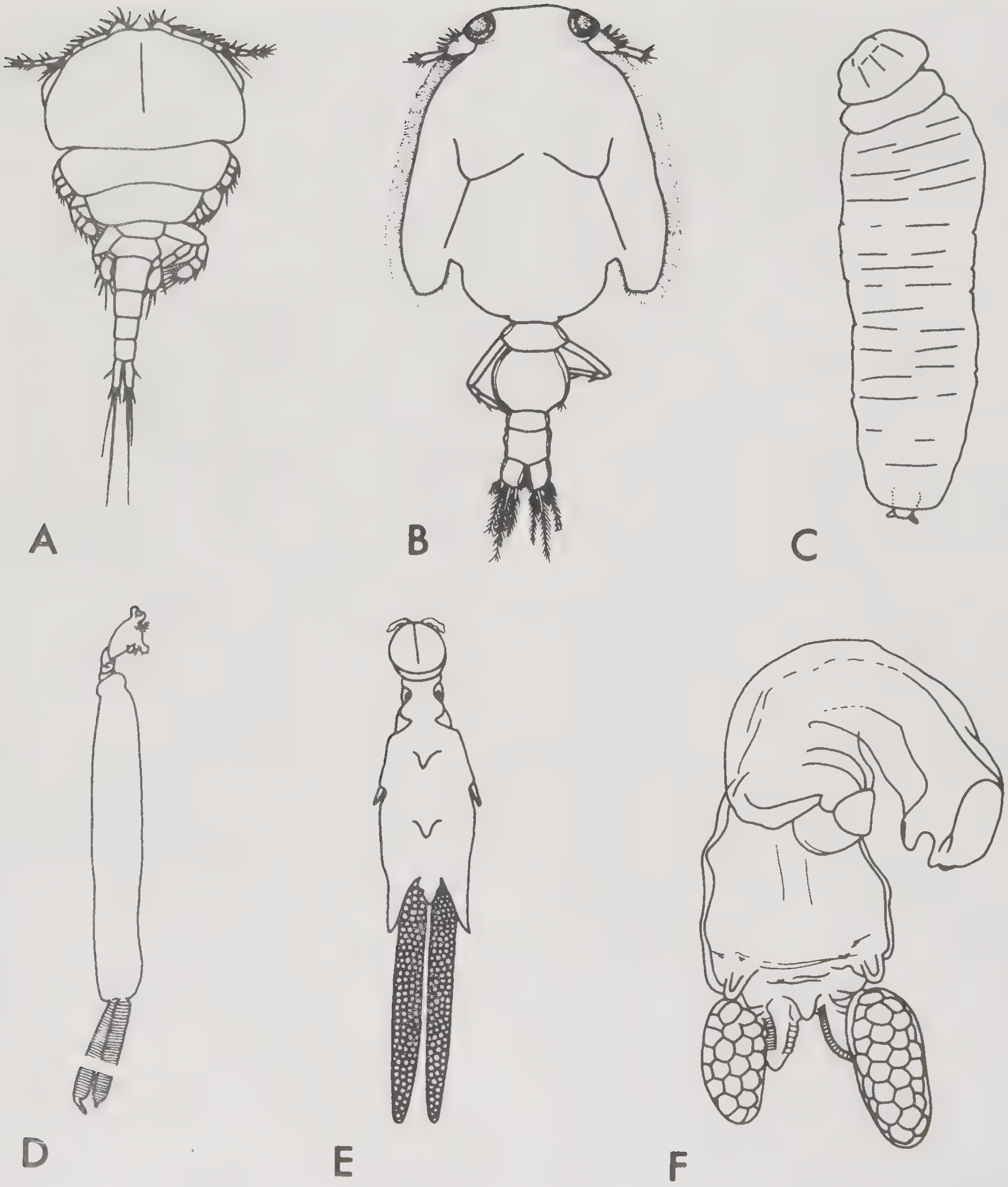

FIGURE 7.—Representatives of the families of ectoparasitic copepods found to infest fishes in the La Jolla area.

A. Bomolochidae (*Bomolochus longicaudus*, female, after Cressey, 1969b);
B. Caligidae (*Caligus hobsoni*, male, after Cressey, 1969a);
C. Dichelesthiidae (*Hatschekia pacifica*, female, after Cressey, 1970);
D. Lernaeidae (*Peniculus fissipes*, female, after Wilson, 1917);
E. Chondracanthidae (*Chondracanthus gracilis*, female, modified after Wilson, 1935);
F. Lerneopodidae (*Epibranchiella septicauda*, female, after Shiino, 1956).

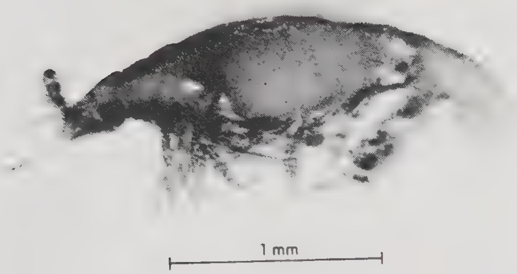

FIGURE 8.—Gnathiid larva from the body surface of the black-and-yellow rockfish, *Sebastes chrysomelas.*

fishes that rarely or never interact with cleaners. In considering the ectoparasites found in the gut of particular señoritas, it would be most meaningful to do so in regard to the ectoparasites known to be hosted by the species of fishes that these particular señoritas were cleaning when collected. Of the 27 cleaning señoritas taken for the gut-content analysis, 15 (56%) were cleaning blacksmiths, 8 (30%) were cleaning topsmelt, 2 (7%) were cleaning garibaldis, and 2 (7%) were cleaning halfmoons. Thus the selection closely parallels the relative frequency with which señoritas were observed cleaning these same species (Table 1) and is a good sample of the fishes that are cleaned by señoritas.

Three species of ectoparasites were collected from 10 blacksmiths, 141 to 199 mm long. Each of these blacksmiths carried from 2 to 39 individuals of the copepod *Caligus hobsoni* on their body surface. One specimen also carried a single gnathiid isopod larva on its body surface, and another the copepod *Clavellopsis flexicurvica* on a gill arch. All 15 señoritas that were collected as they cleaned blacksmiths contained either *Caligus hobsoni* or gnathiid larvae, but no other ectoparasites: one contained gnathiids alone, seven contained *C. hobsoni* alone, and seven contained both gnathiids and *C. hobsoni.* Up to 256 individuals of *C. hobsoni* and up to 263 gnathiid larvae were counted from among the stomach contents of individual señoritas that had been cleaning blacksmiths.

Three species of ectoparasites were collected from 13 topsmelt, 122 to 212 mm long. These topsmelt each carried from 1 to 23 specimens of the copepod *Caligus serratus* on their body surface. Two topsmelt also carried the copepod *Parabomolochus constrictus* on their gills, a single parasite on one, four on the other. Two topsmelt also carried the copepod *Peniculus fissipes* embedded in their fins. Six of the eight señoritas that had been cleaning topsmelt when collected had ectoparasites among their gut contents. Five contained only *Caligus serratus*—as many as 73 in each fish. One other contained only 10 gnathiid larvae, a parasite that was not seen on the topsmelt themselves; however, as noted above, I suspect that this parasite is more widespread than our survey data indicate.

Six species of ectoparasites were collected from 20 garibaldis, 184 to 240 mm long. Nineteen garibaldis each carried 1 to 144 *Caligus hobsoni* on their body surface. Thirteen each carried 1 to 4 individuals of an unidentified species of *Lepeophtheirus* on their body surface, and one carried a single *Bomolochus ardeole* in its branchial cavity. In addition, four carried 1 to 8 gnathiid isopod larvae, two carried a single leech, and one carried a single monogenetic trematode, all on their body surface. The two señoritas that were collected as they cleaned garibaldis had preyed mostly on gnathiid larvae, with each containing over 400 of these parasites. In addition, one had consumed six *Caligus hobsoni,* and the other had taken five *Lepeophtheirus* sp.

Four species of ectoparasites were collected from 13 halfmoons, 166 to 295 mm long. Twelve of the 13 halfmoons each carried 1 to 75 *Caligus hobsoni* on their body surface. Each of two also carried a single *Lepeophtheirus* sp. on its body surface, and each of six carried 2 to 7 *Peniculus fissipes* embedded in its fins. In addition, each of six carried from 2 to 16 monogenetic trematodes on its body surface. Of the two señoritas collected as they cleaned halfmoons, each contained only *Caligus hobsoni* in its gut contents, one a single specimen and the other eight.

Significantly, with the exception of the gnathiid larvae in a cleaner of topsmelt, as discussed above, no parasite was found in the cleaner's gut contents that did not occur on the species of fish that was being cleaned by the cleaner when it was collected. This fact further supports the contention that cleaning tends to be species-specific for a given señorita.

The data clearly show that the parasites most frequently taken by señoritas are certain mobile forms that occur on the body surface of their host. It may be that other parasites on the external body surface are not taken. No leeches or trematodes were found among gut contents, even though these forms are abundant on the garibaldi and halfmoon. Also, the gut contents did not show evidence of the lernaeid *Peniculus fissipes*, an immobile form which partially embeds itself in the skin of its hosts—mostly on the fins. This parasite occurs on topsmelt, garibaldis, and halfmoons among those known to be cleaned by señoritas. However, negative evidence based on the meager gut-content data are weak, especially as the cleaning labrid *Labroides phthirophagus* in Hawaii, which feeds mostly on caligoid copepods, frequently takes lernaeids (Randall, 1958; Youngbluth, 1968). I would expect additional study to show that cleaning señoritas at least occasionally take *P. fissipes*. Nevertheless, several abundant fishes infested by *P. fissipes*, but not found to carry caligids, gnathiids, or other mobile external forms, were not seen being cleaned. For example, the white seaperch is one of the most abundant species at the 3- to 10-m station off La Jolla and yet was never seen being cleaned. Twelve specimens of this fish were examined, and the only ectoparasites found were one to four *P. fissipes* on three individuals. Similarly, the only parasite found on 11 rainbow seaperch, an abundant species in the study areas that was not seen being cleaned, was a single *P. fissipes* on one individual and two on another.

However, not all fishes whose external body surfaces are heavily infested by mobile forms were observed being cleaned. The sheephead, *Pimelometopon pulchrum*, is a case in point. *Caligus hobsoni* occurs on this fish, but only infrequently—a single specimen of this copepod was taken from each of 2 of the 14 sheepheads that were examined. However, the sheephead is heavily infested by two species of *Lepeophtheirus*, a genus of copepods that is closely related to *Caligus*. Up to 70 *L. parvus* were taken from the body surface of a single sheephead, and this fish has not yet been seen being cleaned. Furthermore, up to 4 gnathiid larvae, which cleaners take from other fish, were found on 3 of the sheephead. Similarly, the treefish, *Sebastes serriceps*, which is heavily infested with caligids, has not yet been seen being cleaned. The treefish is not known to carry *C. hobsoni*, but 13 of 15 specimens examined carried up to 12 *Lepeophtheirus longipes* on their body surface, and 3 carried up to 5 gnathiid larvae. The significance of these exceptions to what seems a valid generalization has not been determined. Perhaps it is significant that these two species of fish are not heavily infested by copepods of the genus *Caligus*, as are the more frequently cleaned fishes.

The many parasites that infest the oral and branchial cavities might seem to be potential prey for cleaners, but I found no evidence that these parasites are taken by señoritas.

The principal ectoparasites on the body surface of the two most frequently cleaned fishes, the blacksmith and the topsmelt, are the copepods *Caligus hobsoni* and *C. serratus*, respectively, which are very similar to one another morphologically. With just one exception among the fishes surveyed (discussed below), *C. serratus* seems to be restricted to topsmelt. On the other hand, *C. hobsoni* occurs on a wide variety of species and is also the principal form on garibaldis and halfmoons. Interestingly, a list of the fishes hosting this parasite, ranked by incidence (Table 3), looks much like the ranking of fishes that were observed being cleaned by the señorita (Table 1).

The importance of cleaning in reducing the incidence of ectoparasites on fishes.—Certainly cleaners remove many ectoparasites from the bodies of certain fishes—the numbers in their diet attest to this fact. But does cleaning in fact appreciably reduce the level of infestation on these fishes, or do other parasites quickly replace those that are removed by the cleaners? Although this question is difficult to answer, some insight is provided by observations on the garibaldi. When guarding eggs on their nests during the reproductive season, male garibaldis become especially intolerant of the presence of other fish species. Clarke (1970) recorded the number of times garibaldis, in defence of their territory, attacked fish of various other species at different times of the year. He found that when males were guarding eggs their attacks on señoritas increased elevenfold. Not surprisingly, I saw no cleaning of garibaldis that were guarding eggs. At other times of the year male garibaldis do not guard their territory as vigorously against members of other species and are frequently seen being cleaned. A series of these males were collected both in and out of the reproductive season, and the numbers of ectoparasites they carried were assessed. Seven individuals (mean length 228 mm) sampled as they guarded their eggs carried a mean of 67 *Caligus hobsoni* (range 20-144), 2.5 *Lepeophtheirus* sp., 1.4 gnathiid isopod larvae, and 0.2 monogenetic trematodes. These counts contrast strikingly with those from six males (mean length 219 mm) sampled outside the reproductive season, which carried a mean of only 4.8 *C. hobsoni* (range 0-13), 1 *Lepeophtheirus* sp., 0.8 gnathiid larvae, and no monogenetic trematodes. These findings suggest that males which are guarding eggs become heavily infested with *C. hobsoni* when they do not allow cleaners to approach them, a conclusion strengthened by the fact that over this same period the relative numbers of this same parasite were not noted to change on other infested fishes. The samples included too few of the other parasites to make a meaningful comparison. It remains a question why *Lepeophtheirus* sp. and the gnathiid larvae did not show a pattern of occurrence similar to that of *C. hobsoni*, as both of these parasites are known to be prey of the cleaners. In any event, these data add to the evidence which indicates that *C. hobsoni* is the primary prey of cleaning señoritas in the study areas.

Ectoparasites on Señoritas

Señoritas that were closely observed as they cleaned other fishes often were noted to have caligid copepods on their bodies. One señorita, about 120 mm long, was host to an estimated 100 of these parasites concentrated especially along the dorsal-fin base. These observations were significant because during the survey for ectoparasites, most señoritas taken from the population at large were free of external forms, although many carried a chondracanthid copepod on their gills.

Twenty señoritas, 102 to 190 mm long, were sampled from among those giving no indication of being cleaners. Eight of these carried 1 or more of the chondracanthids on their gills, but only 2, or 10%, had parasites on their external body surfaces: one of these carried 10 specimens of *Caligus hobsoni* and 1 specimen of

TABLE 3.—Hosts of *Caligus hobsoni*.

Species	Specimens examined	Specimens hosting *C. hobsoni*	Number of *C. hobsoni* on each infested fish mean (range)	Percent occurrence
Blacksmith, *Chromis punctipinnis*	10	10	10.6(2-39)	100
Topsmelt, *Atherinops affinis*	13	[1]13	[1]10(3-23)	[1]100
Garibaldi, *Hypsypops rubicunda*	20	19	31.2(1-144)	95
Halfmoon, *Medialuna californiensis*	13	12	19.8(1-75)	92
Opaleye, *Girella nigricans*	10	8	5.4(1-14)	80
Olive rockfish, *Sebastes serranoides*	11	5	2.6(1-4)	45
Blue rockfish, *Sebastes mystinus*	9	4	1	44
Sharpnose seaperch, *Phanerodon atripes*	13	5	2(1-5)	38
Senorita, *Oxyjulis californica*	36	9	11(1-59)	24
Sheephead, *Pimelometopon pulchrum*	14	2	1	14
Rubberlip perch, *Rhacochilus toxotes*	10	1	1	10
Cabezon, *Scorpaenichthys marmoratus*	10	1	1	10
Gopher rockfish, *Sebastes carnatus*	11	1	1	9
Pile perch, *Rhacochilus vacca*	15	1	1	7
Kelp rockfish, *Sebastes atrovirens*	16	1	1	6

[1] *Atherinops affinis* does not carry *C. hobsoni*, but rather is the sole host (with one exception, see text) of the very similar *C. serratus*.

Lepeophtheirus sp.; the other señorita carried a single *Lepeophtheirus* sp. Comparative data were obtained by examining 16 senoritas, 114 to 160 mm long, that had been cleaning. Of these, 11, or nearly 70%, carried copepod parasites on their external body surfaces: 6 carried from 1 to 59 *Caligus hobsoni,* 4 carried from 1 to 9 *C. serratus,* and 1 carried 3 *Lepeophtheirus* sp.

Significantly, those señoritas carrying *Caligus hobsoni* all had been cleaning blacksmiths, those carrying *C. serratus* had been cleaning topsmelt, and the one carrying *Lepeophtheirus* sp. had been cleaning a garibaldi. Thus the ectoparasites found on cleaning señoritas were in all instances forms that also infest the species which that particular señorita had been cleaning. The occurrence of *C. serratus* is especially interesting, because these señoritas are the only fish other than topsmelt found so far to carry this parasite.

Alerted to the phenomenon, I inspected the bodies of many señoritas that incidentally passed by during various phases of the work underwater. Ectoparasites were evident on some, but only on a small minority of the population. That the vast majority are not infested by such parasites accounts for the observation, noted above, that señoritas do not crowd around cleaners that initiate activity in their midst, as do blacksmiths, topsmelt, halfmoons, and others.

On the basis of these data, and on the general cleaning picture that has developed, I believe that at least most of the señoritas infested with caligid copepods are cleaners. Presumably they acquire these parasites while intimately associated with the former hosts during cleaning. That a given cleaner is found to carry parasites similar to those on the fish it has been attending, but no others, is further evidence that cleaning by individual señoritas tends to be species-specific.

Environmental Factors That Influence Cleaning

Temperature.—As noted above, the numbers of señoritas present at the 20- to 25-m station fluctuated in an apparent response to water temperature, with the critical level at about 12° to 13° C. Less cleaning occurred at lower temperatures (Figure 9), which would be expected with fewer señoritas present. Nevertheless, even considering the smaller numbers, the señoritas present at lower temperatures seem less active than those present at higher temperatures. The effect was striking on one occasion at 25 m when, with an influx of warm water, the temperature rose suddenly from 11° to 14.5° C. No change was noted in the numbers of señoritas present over this short period of time, but where no cleaning had been seen during a 20-min survey immediately before, shortly after the temperature rise six different groups of fishes being cleaned were in view simultaneously.

Turbidity.—When the water is turbid because of plankton or suspended sediment, there is noticeably less cleaning activity than when the water is clear. The fishes are generally more wary, and remain closer to cover when visibility is reduced.

Surge.—When there is a strong surge, a frequent occurrence, especially in water less than 10 m deep, there is far less cleaning activity than when the water is still.

Day-night.—The señorita, a strictly diurnal species that takes shelter under cover at night, does not clean after dark.

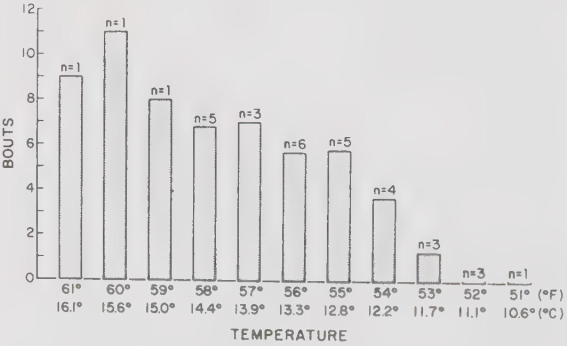

FIGURE 9.—Number of señorita cleaning bouts seen during each of 33 observation periods, 15-25 min long, at different water temperatures in an area 25 m deep at La Jolla. Periods during which temperature fluctuated were not considered. $n =$ number of observation periods at that temperature; where $n > 1$, value given is the mean.

CLEANING ACTIVITY OF THE SHARPNOSE SEAPERCH

Unlike señoritas, which clean as adults as well as juveniles, all of the sharpnose seaperch that I observed cleaning were juveniles less than about 125 mm long. Occasionally noncleaning seaperch swim in groups of 15 or more, but those seen cleaning were always solitary, or in groups of two or three. In agreement with señoritas, cleaning seaperch do not establish well-defined cleaning stations, but instead may clean other fish at any point as they move from place to place. I found no evidence that fishes which are residents of other areas come to where seaperch are located for cleaning; rather, cleaning seaperch occur where resident fishes are numerous. As is true of señoritas, seaperch use the same picking technique to clean material from the bodies of other fish that they use to take small organisms from a benthic substrate. Clearly bottom-picking can be preadaptive to cleaning. Cleaning by seaperch, as by señoritas, usually occurs within 3 m of the substrate. However, there is little overlap in the cleaning areas of the two species: generally seaperch clean at greater depths and/or in colder water than señoritas, where limited observations indicate they may predominate as cleaners even when señoritas are more abundant. Data illustrating this distribution of cleaning activity at a point in time were obtained at the 20- to 25-m and 30- to 35-m locations off La Jolla, where the two species co-occur (Table 4). Despite the fact that señoritas were observed to be far more numerous than perch throughout the depth range of this study (3-50 m), seaperch performed almost all the cleaning observed at the 30- to 35-m location, where cleaning by the much more abundant señorita was limited to a few isolated instances.

TABLE 4.—Number of bouts in which sharpnose seaperch and señoritas, respectively, were seen cleaning other fishes during 15-min observation periods at the 20- to 25-m and 30- to 35-m locations off La Jolla. Two observation periods, one at each location, and never more than 45 min apart, were made on each of the dates indicated.

Date	Number of cleaning bouts observed			
	20- to 25-m location		30- to 35-m location	
	Seaperch	Señorita	Seaperch	Señorita
22 Nov.	2	13	17	0
27 Nov.	0	7	1	0
9 Jan.	2	5	9	0
15 Jan.	2	4	8	0
3 Feb.	2	12	9	2
Total	8	41	44	2

A measure of the incidence of cleaning individuals within the population of juvenile sharpnose seaperch was obtained during 39 observation periods at the 20- to 25-m and 30- to 35-m locations at La Jolla. These observations, totaling more than 26 hr, were made from September 1968 to February 1969. During this period, 201 juvenile seaperch were seen, of which 105, over 52%, were cleaning other fishes. Thus it appears that at least most sharpnose seaperch are cleaners when they are juveniles, whereas only a small minority of the señorita population seem to be cleaners.

Fishes Cleaned by the Sharpnose Seaperch

Because sharpnose seaperch were observed only at depths below 20 m, substantially less data are available on their cleaning activity than on that of señoritas. Of the 105 seaperch observed cleaning during the 39 observation periods reported above, all but one were cleaning blacksmiths; the lone exception was cleaning a solitary blue rockfish, *Sebastes mystinus*. On two other occasions, I saw sharpnose seaperch cleaning rubberlip perch, but otherwise the only fish seen being cleaned have been blacksmiths (Figure 10). Undoubtedly additional observations, especially in other areas, would expand this list. I observed señoritas cleaning in many different areas, but my observations of cleaning seaperch are limited to La Jolla. Clarke et al. (1967) saw a sharpnose seaperch cleaning a rockfish at 150 m off La Jolla, and Gotshall (1967) reported what he believed to be this species cleaning *Mola mola* off Monterey. Yet no matter how many different species the seaperch may in fact clean, there seems no doubt that blacksmiths are prime recipients in southern California, at least in depths shallower than 35 m.

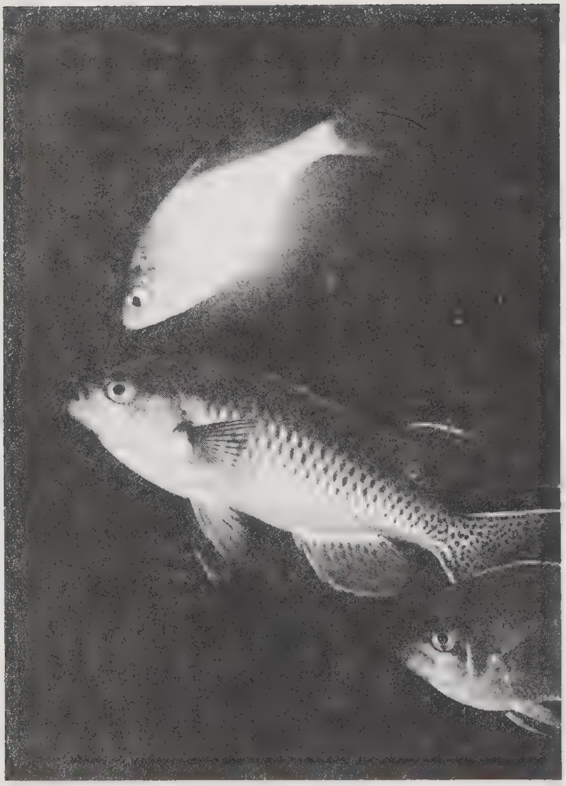

FIGURE 10.—Sharpnose seaperch inspecting a blacksmith, which hovers to solicit cleaning.

Specific Cleaning Interactions—Seaperch-Blacksmith

The limited observations on cleaning by sharpnose seaperch provide details only on interactions with blacksmiths. As nearly as could be seen, when sharpnose seaperch clean blacksmiths the activity proceeds much as it does when blacksmiths are cleaned by señoritas, as described above. However, the observations were too few to determine whether or not cleaning activity is consistently initiated by the cleaner. Several times blacksmiths hovered in their typical head-down posture before seemingly unresponsive seaperch, but perhaps the seaperch had earlier made some initial gesture. Whenever it could be determined, the seaperch initiated the cleaning.

Some details were obtained at the 20- to 25-m location at La Jolla, where two seaperch, known to have been cleaning blacksmiths, were each kept under surveillance for 15 min, while their activity was monitored on tape. Both swam on irregular courses among the rocks but remained within an area encompassing about 15 to 20 m^2. During this time one entered into 4, the other 5, separate cleaning bouts, averaging 2.6 (range 0.5-7.5) and 1.8 (range 0.75-3.5) min long, respectively, all with blacksmiths. The cleaner initiated the activity in each instance, but immediately thereafter a number of other blacksmiths converged on the spot. Most of the cleaning bouts continued after the original blacksmith had left the group, and a succession of others arrived and departed before the bout ended. Although usually they hovered head-down before the cleaners, the blacksmiths nevertheless assumed a wide variety of attitudes. During much of the time they swam with the blacksmiths, the two seaperch under surveillance closely inspected the blacksmith's bodies and actually picked at them 18 and 14 times, respectively. Most of the cleaning was directed at the fin bases, particularly the caudal. While in company with the blacksmiths, one of the seaperch broke away from the group and swam to look closely at the dorsal fin of a blue rockfish. However, no cleaning occurred: the blue rockfish swam away as though uninterested in cleaning and the seaperch returned to the blacksmiths. When not in company with the blacksmiths, the two seaperch swam alone 1 or 2 m over the substrate. One descended to the bottom twice and picked at gorgonians: five times on the first descent, once on the second.

Once a blacksmith was seen obviously attempting to present its caudal fin to a seaperch, without success in enticing the seaperch to clean. Close inspection did not reveal parasites, but part of the fin was torn away and shredded flesh was exposed. Apparently this blacksmith was presenting a point of irritation to the cleaner, which in this instance was an injury, not a parasite. Some cleaners, for example, *Abudefduf troschelii,* which picks molting skin from the Galápagos marine iguana (Hobson, 1969b), will clean dead or injured itssue, but at least on this occasion the seaperch showed no interest.

Material Removed from Other Fish by the Sharpnose Seaperch

To determine the food of cleaning seaperch, I examined the gut contents of 16 specimens, 74 to 122 mm long, that were speared as they cleaned blacksmiths. Food items in their guts, ranked as percentage of each item in the entire sample, were as follows: caligid copepods, 68%; caprellid amphipods, 16%; gnathiid isopod larvae, 9%; algae, 1%; and unidentified items, 6%. Thus ectoparasitic caligids and gnathiids made up 77% of the material. All 16 specimens contained ectoparasites; in fact, ectoparasites constituted the vast bulk of the material in all but one individual, which had fed more heavily on caprellids. As with señoritas, when an appreciable amount of free-living material was present, it was usually sharply divided from the ectoparasites and more digested to the rear in the digestive tract. All the identifiable caligid copepods among this material were *Caligus hobsoni*, which is consistent with what is known of ectoparasites on blacksmiths, the species cleaned by these seaperch, and indicates feeding habits similar to those of the cleaning señorita, presented above.

Incidental Cleaning by a Close Relative

Although sharpnose seaperch were not seen in water less than 20 m deep, the white seaperch, a very similar species, is frequently abundant there. The white seaperch was probably the most numerous of the embiotocids during most of the observations made at the 3- to 10-m location off La Jolla. Underwater the white seaperch and the sharpnose seaperch are nearly identical, but can be distinguished by the dusky bordered caudal fin of the former and the black-tipped pelvics and more pointed snout of the latter.

White seaperch are especially abundant in groups of 10 or more close to surfgrass in 3 or 4 m of water off La Jolla. Typically they hover head-down; in this attitude they are not soliciting cleaning but rather are intently regarding the surface of the vegetation, at which they pick occasionally. Tiny organisms that live on the surfgrass are prey of these fish: five white seaperch, 80 or 81 mm long, speared in this habitat, were filled with (showing percent of total volume) caprellid amphipods (80%), gammarid amphipods (5%), isopods (2%), fragments of algae with encrusting bryozoans (10%), and unidentified crustacean parts (3%). Quast (1968) found that specimens from a kelp bed had fed mostly on small bottom-dwelling crustaceans, polychaetes and bivalves, as well as kelp fragments, some of which were heavily encrusted with bryozoans. Thus the bottom-picking feeding habits of the white seaperch are very similar to the noncleaning habits of the sharpnose seaperch.

On one occasion, I saw a white seaperch swim 1 or 2 m above the surfgrass in company with a lone blacksmith, which hovered head-down in the manner typical of one that desired to be cleaned. The white perch picked at the blacksmith's body several times, but the bout was brief, and the perch soon joined a group of 8 to 10 others of its own kind near the surfgrass below. This seaperch, which proved to be 79 mm long, was speared, and its gut contents included 58 caprellid amphipods, a single gammarid amphipod, one small isopod, plant fragments with encrusted bryozoans, and some unidentified nonparasitic crustacean remains. No ectoparasites were found; its food was similar to that of the other white seaperch reported above. On another occasion I saw a white seaperch cleaning several blacksmiths over a sandy bottom in 12 m of water, but this individual was not collected. Probably the observed cleaning was no more than a brief incidental activity for these fish. At no other time did I see any indication of cleaning by this species, but perhaps the activity is more frequent under appropriate conditions.

CLEANING ACTIVITY OF THE KELP PERCH

Because the kelp perch is not abundant in the La Jolla study area, where larger kelps are sparse, most observations of cleaning by this fish were made incidentally during other projects in areas heavily forested with kelp. However, these other projects generally were centered on the sea floor, whereas kelp perch concentrate above in the midwater and canopy regions. Nevertheless, observations of cleaning were sufficiently frequent to recognize this species as a habitual cleaner, though probably less so than either the señoritas or the juvenile sharpnose seaperch. In taking material from the bodies of other fishes, the kelp perch uses the same picking technique that it employs to pick items from an algal substrate, or that are adrift in midwater. Its pointed snout and dentition, which is similar to that of the señorita, as described above, are well suited to cleaning.

Insofar as an aggregation of kelp perch tends to remain in one location, these fish can perhaps be regarded as maintaining a station at which other fishes are cleaned. But I saw no indication that more than one or a few members of a given aggregation clean, or that other fishes come to these locations from any distance for cleaning. In fact, I saw only blacksmiths and other kelp perch being cleaned by this fish. In the one observation of intraspecific cleaning, a single kelp perch swam among others of its aggregation, intently inspecting their bodies. Usually the subject of this attention moved away, whereupon the cleaner moved to another fish. A few responded to the cleaner by erecting their fins and hovering immobile in a head-down posture, and these were cleaned. Occasionally a fish being cleaned suddenly darted away as if the cleaner had been too vigorous in its attentions. All blacksmiths being cleaned were solitary individuals that hovered in head-down soliciting fashion close to an aggregation of kelp perch. Whether or not one of the perch had earlier made an initiating overture was never determined. Never more than one or two of the perch in the aggregations were seen cleaning these blacksmiths. Occasionally a cleaner would closely follow a halfmoon or kelp bass that incidentally passed close by, but I saw no evidence that these fish were interested in the perch, and no cleaning occurred.

Three kelp perch, 94 to 99 mm long, one of which had been cleaning a blacksmith, were collected from an aggregation hovering near a stand of feather-boa kelp. The gut contents of the individual known to have cleaned the blacksmiths contained (showing the percent of total volume): gnathiid isopod larvae (50%), nonparasitic isopods (5%), gammarid amphipods (5%), caprellid amphipods (20%), and unidentified material (20%). Neither of the two that were not known to have cleaned contained evidence of ectoparasites: one was full of caprellid amphipods (90%) and unidentified material (10%), whereas the other had nothing in its digestive tract except a few unidentified fragments posteriorly.

Limbaugh (1955) reported kelp perch cleaning kelp bass, opaleyes, garibaldis, blacksmiths, and walleye surfperch (*Hyperprosopon argenteum*).

DISCUSSION

Various cleaning fishes remove a wide variety of deleterious material from the bodies of the animals they service. In addition to ectoparasites, this material includes diseased, injured, or necrotic tissue, fungi, and unwanted food particles (Feder, 1966; Hobson, 1968, 1969b; and others). However, the discussion below considers cleaning only as the removal of ectoparasites, because my data indicate that these are the only items taken in significant amounts from California fishes by the cleaners considered in this report.

INCIDENTAL VS. HABITUAL CLEANING

Cleaning is widespread among small-mouthed marine fishes that characteristically pick minute organisms from the substrate (Hobson, 1968). Included are species of the families Chaetodontidae, Pomacentridae, Labridae, Embiotocidae, Blenniidae, and others. Morphological and behavioral characteristics suited to their way of life have preadapted many species of these families for the cleaning habit. Probably some such fishes pick ectoparasites only incidentally during routine foraging when under certain conditions the body of an adjacent fish, infested with ectoparasites, becomes accessible as just another feeding substrate. The relative tendency of a given species to clean likely is influenced by both short-term and long-term environmental changes. Such changes may be expected to alter interspecific relations, by affecting not only the relative availability of various prey organisms and the incidence of various ectoparasites, but also the species composition of the interacting fishes themselves.

In California the white seaperch likely is one of those species that cleans only occasionally as an incidental adjunct to regular foraging. Several other California species reported by Limbaugh (1955) and Gotshall (1967) clean, including black perch, pile perch, and rainbow seaperch, but they have not been seen doing so by me. The report of cleaning by the blacksmith (Turner et al. 1969) remains an anamoly, as this fish does not fit the pattern of a bottom-picking predator described above. However, it may be significant that many of those substrate-picking predators which clean most frequently are species that also feed on material adrift in midwater, as do the señorita, sharpnose seaperch, and kelp perch. Thus this mode of feeding too, including the taking of plankton, may, in some species, favor adaptations that are suited to cleaning. Fishes that are adapted to both substrate-picking and plankton-picking may possess adaptations especially well suited to cleaning.

Probably many species of fishes clean incidentally on isolated occasions, but relatively few are habitual cleaners. And even the habitual cleaners vary greatly in the degree to which they are specialized for this habit. Species of the Indo-Pacific labrid genus *Labroides* are highly specialized cleaners that feed almost exclusively on ectoparasitic crustaceans (Randall, 1958; Youngbluth, 1968). These fishes possess many specific morphological and behavioral specializations that are adapted to this way of life (Feder, 1966; Losey, 1971). However, only a small minority of cleaners are so highly specialized; most are but part-time practitioners of the cleaning habit, with much of their food being derived from other sources.

That some cleaners depend on ectoparasites for prey, whereas others can subsist equally well on food from other sources, has led to classifying various species as either obligate or facultative cleaners (e.g., Youngbluth, 1968). The señorita, sharpnose seaperch, and kelp perch may well resist being so classified because their cleaning seems to be characteristic not so much of a species as of just certain individuals. At least at a given time, most señoritas do not clean, whereas some seem to be facultative cleaners, and a few might even be obligate cleaners. Juvenile sharpnose seaperch follow a similar pattern, but with a relatively higher incidence of individuals that clean. Limited data can only suggest that the status of the kelp perch may be similar.

CLEANING INITIATED BY THE SEÑORITA

Usually there seem to be fishes present that need cleaning, as shown when a señorita identifies itself as a cleaner by initiating action with, say, a blacksmith or a topsmelt, and immediately is converged upon by many other fish that crowd in its way seeking attention. That such fishes generally wait for a señorita to begin the cleaning, rather than attempting to initiate activity themselves with one of the many señoritas present, likely reflects a low probability of success if they make the first move. If, as it seems, the vast majority of señoritas are not cleaners, or at least not currently predisposed to clean, then random efforts to solicit service would not seem adaptive.

This situation contrasts with that of the Hawaiian wrasse *Labroides phthirophagus*, of which all individuals seem to be obligate cleaners (Youngbluth, 1968), and which is not nearly as abundant on Hawaiian reefs as the señorita is in California. In centering their activity around well-defined stations, the distinctive *L. phthirophagus* can be recognized readily by others that need cleaning. Thus, not surprisingly, cleaning encounters that involve *L. phthirophagus* are regularly initiated by fishes seeking cleaning (Losey, 1971).

We have seen that under certain circumstances various fishes initiate cleaning encounters with señoritas. Some fishes successfully do so by hovering amid unusually dense concentrations of señoritas, but the overtures of such fish are not directed at individuals; rather, they are broadcast to the assemblage at large. The success of this tactic presumably follows the probability that an individual predisposed to clean occurs among such a large number of señoritas.

Kelpfish regularly solicit cleaning from individual señoritas, but the situation is exceptional. Because kelpfish rise into midwater for cleaning, it appears that they do not receive satisfactory service in their regular habitat amid benthic vegetation. In their usual surroundings, where they are extremely difficult to discern, the cryptic kelpfish may be relatively inaccessible to cleaning señoritas. One can see why a fish thus handicapped might be required to initiate needed cleaning itself. The number of unsuccessful attempts experienced by kelpfish before a señorita was finally induced to clean them underscores the existing problem of locating a cleaning individual.

SPECIES-SPECIFIC CLEANING

Because the cleaning señorita initiates most of its activity, it has the opportunity to select its clients, and the data indicate that a species-specific choice is exercised. That individual cleaners tend to limit their selection to members of only one species may be related to the fact that they initiate cleaning on the home ground of the fishes they serve, when these fishes are engaged in some of their regular activity. As each of these clients has distinctive habits, a señorita approaching to clean a fish of one species faces a somewhat different situation than a señorita approaching to clean a fish of another species.' The distinctions often are subtle, but may be significant enough to account for a given señorita's tendency to seek out members of only one species.

Again we can draw a contrast with the cleaning behavior of *Labroides phthirophagus*, individuals of which receive members of many different species at well-defined cleaning stations (Randall, 1958; Youngbluth, 1968). Probably such nonspecific cleaning is characteristic of cleaners whose activity is confined to these established locations. Fishes that visit such cleaning stations enter the cleaner's own territory, and frequently join a mixed-species group that hovers in wait for service. In tending these fishes on its home ground, the cleaner is receiving them on its own terms, so to speak, so that the situations surrounding cleaning bouts with all of the different species are essentially the same.

Cleaning by the señorita may not be species-specific on those few occasions when the cleaning activity is initiated by the fish in need of such service, for example by the kelpfish, as described above. Although they show some difficulty locating a receptive señorita, kelpfish nevertheless seem far more successful at doing so than one would expect if indeed they are required to find one that will clean only kelpfish. Thus, although individual señoritas seem to be species-specific when they themselves initiate cleaning, they may be considerably less so, and perhaps even nonspecific, when the other fish makes the initial overture. There are no data on this point, however.

The extent to which these considerations apply to juvenile sharpnose seaperch and kelp perch cannot be ascertained because data are lacking.

SIGNIFICANCE OF POSTURES ASSUMED BY FISHES THAT SOLICIT CLEANING

When members of an assemblage of fishes like blacksmiths or topsmelt converge on a cleaning site that has developed in their midst, probably their attention was initially alerted by the unnatural-appearing posture assumed by the individual first approached by the cleaner. Usually this posture does not seem to be assumed purposefully, but rather results when the fish, having ceased swimming and immobilizing its fins, passively drifts out of its regular attitude (Hobson, 1965b). The posture thus assumed varies, especially between species, where perhaps differing centers of gravity are determining factors. Thus the blacksmith usually hovers head-down, whereas the topsmelt is more often tail-down. Sometimes an unnatural-appearing posture is actively assumed when the fish attempts to present to the cleaner a certain part of its body, presumably that part carrying an irritation. By virtue of their unusual appearance, these postures in cleaning interactions serve to draw attention to the fish that is cleaned. It does not seem necessary that any particular posture be assumed, only that it look out of the ordinary. Reports are widespread (see Feder, 1966) of cleaning recipients assuming these unnatural-appearing postures.

Attention-getting postures assumed by fishes being cleaned probably occurred incidentally during the early development of cleaning symbiosis, when fishes hovering to be cleaned quite naturally stopped moving and passively drifted out of their regular attitudes. As the various cleaning relations evolved, apparently this obvious cue subsequently assumed a different role as a signal in different situations. Generally these postures are suggested to be signals between the recipient of cleaning and the cleaner, indicating a readiness to be cleaned. Quite likely this is the primary signal-function in activity involving such cleaners as *Labroides phthirophagus,* where all members of the species are cleaners and where activity is centered around cleaning stations that are well known to other fishes in the area. In this situation a fish in need of cleaning should be reasonably successful in advertising its condition by assuming the characteristic soliciting posture before a fish recognizable as a cleaner. Losey (1971) showed that various fishes regularly employ this tactic to induce *L. phthirophagus* to clean them. Observations in the Gulf of California demonstrated that the cleaning station itself has played a role in establishing the soliciting posture as a cue. There I have seen the goatfish *Mulloidichthys dentatus* hovering head-down at cleaning stations of the butterflyfish *Heniochus nigrirostris,* when the resident cleaner was itself temporarily absent. Losey (1971) observed similar behavior among Hawaiian fishes. In such a situation the hovering posture probably alerts the cleaner to fishes that have arrived for cleaning.

However, in cleaning activity involving the señorita, the soliciting posture usually is assumed only after cleaning has been initiated by the cleaner. The problem of recognizing an individual that will clean among the vast majority of señoritas that do not clean, coupled with the absence of well-defined cleaning stations, would reduce the adaptiveness of the client's soliciting posture as a cue to initiate cleaning. Probably the most effective way for a fish to obtain needed cleaning in this situation is to wait until a cleaner has identified itself by initiating activity with some fish in the area. Once this has occurred, one can see the value of the posture, when assumed by the first fish to be approached, as a cue in alerting other fish that need cleaning to the presence of a cleaner. In effect, then, the fish assuming the soliciting posture advertises the temporary existence of the transient cleaning "station" to other potential recipients of cleaning. Well-defined cleaning stations like those of *Labroides phthirophagus* do not need this sort of advertisement, as their locations are well known to the fishes that visit them. Nor is it necessary that cleaning individuals of *L. phthirophagus* be pointed out, as all members of that distinctive species are cleaners. Despite this, it is probable that fishes hovering to be cleaned at a *Labroides* station themselves create a visual cue that tends to attract other fishes.

There may also be a maladaptive aspect to the postures assumed by fishes that solicit cleaning. In hovering at an unnatural angle, fins immobile and erect, a fish may enhance its chances of being cleaned, but it would also seem likely to draw the attention of predators and to handicap itself in evading attack. Perhaps such an increased vulnerability accounts at least in part for the sharp decline in cleaning that occurs with reduced visibility, when predators can approach closer undetected. Increased vulnerability may also account for the observation reported earlier (Hobson, 1965c), where pomadasyids in the Gulf of California abruptly broke away from cleaners when a predator approached.

THE POSSIBILITY THAT FISHES BEING CLEANED EXPERIENCE STRESS

Being prodded and picked over by an animal of another species would seem to require a difficult adjustment for a fish. It may well be that fishes experience stress under this circumstance, even when the behavior is well established. Certainly observations have shown that this experience can be uncomfortable, judging from how often fishes being cleaned suddenly bolt forward, and swim away, apparently having been nipped too vigorously by the attending cleaner. Sometimes too, a fish approached by a cleaner clearly experiences conflicting responses, one moment tolerating or even soliciting the cleaner's attentions, and the next moment chasing it away on each approach. Such ambivalent behavior was especially evident in rubberlip perch. Losey (1971) noted that *Labroides phthirophagus* in Hawaii is sometimes attacked by fishes that it attempts to clean, and suggested that this may occur when the cleaning is painful to the host fish.

The color changes shown by many fishes being cleaned (Randall, 1958; and others) may in fact be manifestations of stress. It is well known that many fishes experience color changes in response to stress. Earlier (Hobson, 1965a) I discussed the striking color change of the goatfish *Mulloidichthys dentatus* when it solicits cleaning in the Gulf of California, and pointed out that this fish shows the same color change in other situations that are obviously stressful. Such color changes have been regarded as signals between the fishes being cleaned and the cleaners, (e.g., Feder, 1966), functioning in the cleaning interaction much like the soliciting attitudes discussed above. As with the attitudes, any role such color changes may now have assumed as a signal probably evolved from an incidental byproduct of early cleaning. I have no data on this point relating to the California species, as such color changes are not especially evident in fishes that were observed being cleaned there.

ARE CLEANERS IMMUNE FROM PREDATION?

Reportedly some cleaners are immune from predation because of the service they provide the predators (Feder, 1966; and others). Limbaugh's (1961) belief that the señorita enjoys such immunity is based on observations of this labrid entering the open mouth of kelp bass to clean and on not finding it among the stomach contents of predators during a food-habit study. However, Quast (1968) found señoritas in the stomachs of kelp bass, and H. Geoffrey Moser, U.S. National Marine Fisheries Service (unpublished data), found señoritas in stomachs of the bocaccio, *Sebastes paucispinis*, and the starry rockfish, *S. constellatus*.

I doubt that cleaners enjoy immunity in the sense that predators, recognizing them as benefactors, actively avoid preying on them. Cleaners may recognize those predators which are not at that time intent on feeding and may restrict their cleaning to such individuals. A predator that assumes a soliciting posture may effectively advertise this situation, and no doubt other cues exist. Such mechanisms would reduce the chance of cleaners placing themselves in vulnerable situations while cleaning. In addition, cleaners probably are not as vulnerable while cleaning large predators as might be expected simply because cues characteristic of feeding situations are not present. In associating themselves so intimately with predators, cleaning fishes show behavior that is so unlike that of prey that predators probably do not regard them as food. However, even if such factors do reduce the danger that might seem inherent in the cleaning act, I doubt that their cleaning role affords these fishes any security from being eaten in noncleaning situations.

PARASITES AS PREY OF THE CALIFORNIA CLEANERS

It is hardly surprising that the fishes which are cleaned most frequently in California are those which are the most abundant and at the same time carry the most ectoparasites. Thus the blacksmith, topsmelt, halfmoon, and garibaldi are the fishes cleaned most frequently, and the survey of ectoparasites showed them to be among the most heavily parasitized. The vast majority of ectoparasites on these particular fishes are mobile forms, mostly caligid copepods and gnathiid isopod larvae, that occur on the body surface of their hosts. That these same parasites were found to make up the diet of the cleaners attending these fishes is consistent with the observation that only the exteriors of fishes were seen being cleaned during this study.

Although the forms infesting the external body surface are the most numerous ectoparasites on the fishes available to the California cleaners, many other types were found to infest the oral and branchial cavities. One might question why these other parasites do not seem to be taken, especially as Limbaugh (1955, 1961) reported señoritas entering the mouth of the kelp bass and cleaning beneath the gill covers of the garibaldi. Furthermore, such behavior has been widely reported for some other cleaners, such as species of *Labroides* (Eibl-Eibesfeldt, 1955; Randall, 1958; and others), and some echeneids are known to habitually feed on copepods from the branchial cavities of sharks (Cressey and Lachner, 1970). Nevertheless, any such activity by señoritas must be relatively rare. In discussing this situation I limit my remarks to the señorita, because data are presently insufficient to determine whether the same may apply to the sharpnose seaperch and kelp perch.

Señoritas would not be expected to take parasites from the oral or branchial cavities as often as species of *Labroides* or echeneids if for no other reason than they simply are too large relative to most of the fishes they clean. Whereas species of *Labroides* or the echeneids are small enough to enter the oral and branchial cavities of most of the fishes they service, the señorita is nearly as large, and sometimes even larger, than most of its clients. Significantly, Limbaugh observed señoritas cleaning within the oral and branchial cavities of kelp bass and garibaldis, both of which are relatively large species. Most of the señorita's cleaning is directed toward smaller species, like the blacksmith and the topsmelt.

The specialized techniques that would be required to prey on the parasites of the oral and branchial cavities would probably pose another problem to the señorita. In its regular habit of taking parasites from the external surfaces of fishes, the cleaning señorita concentrates on just a few forms that not only are numerous on many of the most abundant fishes, but also are not too dissimilar from free-living prey of the species. Sometimes these external forms also occur in the branchial cavity, and some similar forms, e.g., bomolochids (Figure 7), habitually occur there and in the oral cavity. But the majority of parasites characteristic of the branchial and oral cavities are aberrant forms, e.g., dichelesthiids, chondracanthids, and lerneopodids (Figure 7), and these are unlike anything else encountered by the señorita. No one type predominates; rather, they occur in a wide variety of forms, none widespread among the different species of fishes, and none especially abundant (except on an occasional individual fish). Thus a cleaner probably could not subsist on one type alone but would have to master a repertoire of specialized techniques in order to exploit enough of these varied forms to make it worthwhile. And before access is gained to the site of infestation, a much more refined cleaner-host interaction must have evolved than is necessary when parasites are simply cleaned from the external body surface. No such relation would evolve unless the cleaner acquired the precise manipulations necessary to pick attached parasites off the gills without damaging the delicate gill membranes. Obviously the cleaning relation would not be adaptive if such damage occurred. In short, to feed habitually on parasites from the oral and branchial cavities would seem to require a higher degree of specialization than has been demonstrated by the señorita. It seems unlikely that such specialization would develop as long as the more abundant and readily available forms on the body surfaces continue to satisfy the cleaning needs of the species. Certainly judging from the way blacksmiths, topsmelt, and other fishes vigorously compete to have their external parasites removed, it would seem that there is little immediate chance of these parasites falling into short supply.

CLEANING SYMBIOSIS AND THE DISTRIBUTION OF SHORE FISHES

In his often-cited report on cleaning symbiosis, Limbaugh (1961: 48) stated:

> In my opinion it is the presence of the señorita and kelp perch that brings the deep-water coastal and pelagic fishes inshore to the edge of the kelp beds on the California coast. Most concentrations of reef fishes may similarly be understood to be cleaning stations. Cleaning stations would therefore account for the existence of such well-known California sportfishing grounds as the rocky points of Santa Catalina Island, the area around the sunken ship *Valiant* off the shore of Catalina, the La Jolla kelp beds and submarine canyon and the Coronado Islands.

Presumably this conclusion was intuitive, as no data were presented. In his review of cleaning symbiosis, Feder (1966: 368), basing his conclusion on Limbaugh's work, similarly stated: "In all probability, many good fishing grounds are such primarily because they are cleaning stations." I believe that this contention is unfounded. Señoritas are the major cleaners in California inshore waters, so that if cleaning symbiosis does account for most concentrations of reef fishes in this region, as Limbaugh suggested, then señoritas would be the cleaner largely responsible. Cleaning occurs wherever señoritas are concentrated but clearly is not a major activity of the population, even though it may be so for a relatively few individuals. In any event, it seems safe to conclude that cleaning is not among the major factors determining the distribution of señoritas. And if cleaning does not determine the distribution of señoritas themselves, it seems unlikely that it would determine the distribution of other species.

Undoubtedly many factors contribute to creating situations that draw concentrations of fishes to certain locations. Where a number of different species have similar requirements, assemblages will develop where conditions satisfying these requirements are optimum. The presence of these fishes increases the complexity of the environment, thus creating situations that support still other species, and so on. Often it is apparent that certain features are especially significant as a basis for these concentrations. Consider, for example, the rocky points that Limbaugh included in his list of "well-known California sport-fishing grounds." The flora and fauna of these locations are generally rich, a fact probably related to such local features as converging currents that frequently produce upwelling and nutrient-rich waters. Plankton is commonly abundant here, along with plankton-feeding fishes like the blacksmith. Señoritas and other species frequently are numerous here too, but the main attraction seems to be a generally rich food supply rather than available cleaning. Similarly it is unrealistic to attribute concentrations of fishes around sunken ships to cleaning activity. Where a wreck has settled on an open expanse it becomes a haven for fishes that require a nearby structure for cover or a spatial reference point. Obviously such fishes will center themselves here, because the surrounding featureless substrate does not meet their requirements. I am describing a well-known phenomenon, one that is the rationale behind constructing artificial fishing reefs. Thus food and a suitable substrate often appear to be key features in a habitat that supports large numbers of fishes. Of course to cite just one or the other would be an oversimplification, as requirements in both must be satisfied, along with many other perhaps more subtle needs. The various species assembled at such locations interact in a variety of ways; cleaning symbiosis is one such interaction, and undoubtedly an important one, but hardly the prime reason for them being there.

CHANGES IN HABITS WITH TIME

Uncertainty remains regarding changes in habits with time. The picture of activity developed in this report was derived directly by observing activity and also indirectly by examining both digestive-tract contents and the specific ectoparasites that infest the various fishes. But these methods only define situations that exist over a relatively brief span of time. Data on individual activity over longer periods are needed. Certainly habits of individuals change with time, but how much change and over how much time? The fact that material in the digestive tracts frequently occurs in sharply delimited homologous blocks indicates that these fishes often feed heavily or even exclusively on one particular type of prey, and then abruptly shift to something else. Are habits such as a relative tendency to clean and to clean members of just one species immutable characteristics of individuals, or have the observations described in this report simply defined temporary situations that the various individuals just happened to be experiencing at the time they were singled out for study? It is possible that all señoritas clean at one time or another, though not all at once, and only a few at a time. It is also possible that a señorita, which tends to clean members of just one species during a given period of cleaning, may select members of another species during a subsequent period of cleaning. Despite these questions, the conclusions drawn in this report are dependent only on an accurate assessment of the immediate situation, so that their validity is not affected by whether or not the habits of individuals under study remain basically unchanged over time.

A NOTE ON INDIVIDUAL VS. SPECIES HABITS

Information on variations in feeding behavior among individual fish under natural conditions is difficult to acquire. Typically a given behavior is described as a species characteristic, and the extent to which this behavior varies among the different members of the species is unknown. Observations of cleaning by the señorita demonstrate that different individuals in a population may react differently to a given situation. Unquestionably this phenomenon extends beyond cleaning behavior to other facets of the animal's activity. If, as is probable, some of the characteristics of individual fish result from early imprinting, then different members of the same population could be expected to react differently in certain situations throughout life. In any event, it seems unquestionable that the behavior of an individual is considerably more limited than that descriptive of its species, or even its own population.

CONCLUSIONS

1. Three inshore species of fishes in southern California are habitual cleaners: the señorita, the sharpnose seaperch, and the kelp perch. A number of other species clean occasionally as an incidental adjunct to their regular feeding.

2. The señorita may clean throughout its postlarval life, whereas cleaning by the sharpnose seaperch is an activity largely of juveniles. The life-history period during which kelp perch clean has not been defined.

3. Cleaning is of secondary significance to these species, although it may be of major significance to certain individuals. Only a few of the many señoritas present at a given time clean, and the same seems to be true of the kelp perch. The incidence of cleaners is much higher among juvenile sharpnose seaperch, but the adults of this species do not seem to clean regularly. The major food of all three species is free-living organisms which they pick from a substrate and midwater.

4. There is little overlap between the cleaning areas of the three species. The señorita is the major cleaner in southern California inshore waters by virtue of its great abundance in a variety of rocky habitats. However, the kelp perch may be the predominant cleaner in the canopy region of the kelp beds, where the species concentrates, and the sharpnose seaperch is the predominant cleaner where it occurs at depths below about 20 to 30 m and/or water under 12° or 13° C, even though the señorita may be more abundant.

5. The señorita and sharpnose seaperch do not establish well-defined stations at which they receive other fishes seeking to be cleaned—a situation frequently described for other cleaner fishes. Rather, as they move from place to place, individuals of these species approach and clean other fishes in various different locations.

6. Cleaning activity by these species is essentially limited to removing ectoparasites from the external body surfaces of fishes. They do not ordinarily take parasites of the oral and branchial cavities. The dentition of the señorita and kelp perch, which is similar and which includes a number of long, curved canines that project forward at the front of each jaw, seems especially suited to pick ectoparasites.

7. The major prey taken by these fishes through cleaning are caligid copepods and gnathiid isopod larvae. The species of parasite taken most often by the señorita and sharpnose seaperch is *Caligus hobsoni.*

8. Some species of fishes are cleaned far more often than others, and many species that cooccur with these cleaners are not cleaned at all. The fishes most frequently cleaned are those which at the same time are most abundant and most heavily infested with ectoparasites. The most numerous ectoparasites on these fishes are caligid copepods, the most abundant of which is *C. hobsoni.*

9. Cleaning effectively reduces the number of ectoparasites that infest the external body surfaces of fishes that interact with the cleaners.

10. At any given time, many individuals of the more frequently cleaned species are in need of cleaning. Nevertheless, in activity involving the señorita, infested fishes do not ordinarily attempt to initiate cleaning but instead wait for cleaning to be initiated by the cleaner. Because the vast majority of señoritas are not cleaners, or at least are not currently predisposed to clean, random efforts to solicit cleaning from señoritas in the population at large would not be adaptive.

11. When initiating its cleaning activity, a given individual señorita tends to approach and clean members of only a single species of fish.

12. Because the vast majority of señoritas are not currently predisposed to clean and because there are no well-defined cleaning stations, the unnatural-appearing posture assumed by a fish approached by a cleaner is an important cue in advertising the location of available cleaning to other fish in need of this service.

13. Fishes being cleaned probably experience some degree of stress. The color changes exhibited by some fishes when being cleaned are essentially manifestations of this stress; secondarily, they may have assumed a signal-function in certain cleaning interactions.

14. While intimately associated with the fishes they clean, señoritas frequently become infested themselves by the same parasites they are attempting to remove from these other fishes.

15. Cleaning activity is sharply curtailed when visibility is reduced by turbid water or when there is strong water movement, such as a heavy surge.

16. Cleaning activity among these fishes is a diurnal phenomenon. There is no evidence that it continues after dark.

17. Any so-called "immunity" from predation that a cleaner may enjoy probably relates (1) to an ability to recognize predators that are not intent on feeding and to limit cleaning to such individuals, and (2) to the fact that behavior exhibited by a cleaner servicing a predator is so unlike that of prey that the predator does not regard the cleaner as food. However, their role as cleaners probably does not afford these fish any security from being eaten during noncleaning situations.

18. Cleaners are widespread among small-mouthed marine fishes that characteristically pick tiny organisms from a substrate. This mode of feeding, especially when combined with the capacity to pick tiny prey that are adrift in midwater, preadapts fishes to the cleaning habit.

19. There is no basis for the contention that many of the good fishing grounds in southern California are such because fishes have congregated to be cleaned by resident cleaners.

20. Feeding behavior varies significantly among individuals of at least some species. Thus the habits of an individual can be more limited than those descriptive of its species or even its own population.

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SUSTAINED SPEED OF JACK MACKEREL, *Trachurus symmetricus*

John R. Hunter[1]

ABSTRACT

Jack mackerel, *Trachurus symmetricus*, were forced to swim for up to 6 hr at various speeds in an activity chamber. The probit estimate for the swimming speed at which 50% of *Trachurus* would fatigue during 6 hr was 93.4 cm/sec (8.4 *L*/sec) for fish 10.0 to 11.9 cm and was 22.4 $L^{0.6}$/sec for fish 9.0 to 17.6 cm where *L* is the total length of the fish in centimeters. At higher speeds, *Trachurus*, 15 cm, swam for 3 min at 160 cm/sec or 10 *L*/sec. The swimming speed at which 50% fatigued declined exponentially with time for about the first 22 min of swimming and thereafter declined linearly with time. The possible significance of the time-speed relationship for *Trachurus* is discussed.

Although a substantial literature on the swimming speed of fishes exists (see Bainbridge, 1958; Gray, 1968), few reliable estimates of maximum sustained speed exist. Much of the literature on swimming speed of fishes is concerned with estimates of maximum speed or burst speed, that is, speeds that can be maintained for only a few minutes or less. A sustained speed implies, on the other hand, that the animal is capable of swimming at that speed for hours. For example, Brett (1967) recommended a minimum of 200 min for a fixed sustained speed test. Fairly wide agreement exists that 2 to 3 *L*/sec can be maintained for an hour or more and salmonids and herring seem capable of sustaining 3 to 4 *L*/sec for such periods (Blaxter, 1969). These conclusions were drawn primarily from studies of freshwater fish and salmon; no estimates of maximum sustained speeds have been made for fast-swimming pelagic marine forms. The object of this study was to determine the sustained speed threshhold of jack mackerel, *Trachurus symmetricus*, a pelagic marine fish of commercial importance. The body form and musculature of *Trachurus* appear to be designed for greater hydrodynamic efficiency at high speeds than other species heretofore studied. In *Trachurus*, lateral musculature is concentrated in the anterior portion of the trunk, and inserts by tendons on a small deeply forked caudal fin.

In addition to the interest in comparing the sustained speed capabilities of *Trachurus* with that of fish with other body forms, sustained speed data have significance in prediction of migratory capabilities and physiological limits.

APPARATUS AND METHODS

The apparatus used in the experiments was an activity chamber provided with a water current of various calibrated speeds. The apparatus was the same as the one described and figured by Hunter and Zweifel (1971) in this issue except that a port was provided in the transparent hatch of the swimming chamber so that fatigued fish could be removed by hand from the downstream screen without reducing the flow in the chamber. The error in estimating the water speed in the swimming chamber did not exceed 10% and it was assumed that the fish were swimming at the estimated speed.

The experimental design was essentially the same as that used by Brett (1967) for determining the sustained speed threshhold for sockeye salmon, *Oncorhynchus nerka*. Fifty-five groups of five *Trachurus* (9.0 to 17.6 cm total length, mean = 12.43 ± 0.11 cm) were subjected to a fixed speed of 38 to 160 cm/sec for 360 min or longer after an introductory period of about 30 min at a low speed. A time-lapse camera photographed the fish at 1-min intervals and the time to fatigue for each fish was determined from the photographs. The temperature of the water in the activity chamber and in the holding

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tank (a plastic swimming pool 15 ft in diameter) was maintained by a temperature regulation system at about 18.5° C. The mean test temperature was 18.48 ± 0.03° C. The fish were captured near Santa Catalina Island, Calif., on 12 September 1969. Tests began 2 weeks later and ended on 21 November 1969. Fish were fed an abundant ration of chopped squid, anchovies, and frozen brine shrimp. Probit analysis, a statistical technique first applied to sustained speed data by Brett (1967), was used to estimate sustained speed threshholds.

Variability in length posed a problem in the analysis. Although all fish were from the same school, differences in length existed; also the fish grew in the course of the study. These differences were insufficient, however, to determine the form of the relationship between length and sustained speed. In general, the relationship between length and sustained speed for other species (Bainbridge, 1962; Brett, 1965), theoretical considerations (Gray, 1968; Fry and Cox, 1970), and relationships between length and other swimming capabilities (Magnuson, 1970), indicate that speed is proportional to a fractional power of length equal to about $L^{0.6 \pm 0.1}$. In addition, the minimum swimming speed of *Trachurus* was proportional to $L^{0.6}$ when estimated from Magnuson's equation (Hunter and Zweifel, 1971). In light of the above evidence it seemed preferable to use 0.6 as the coefficient of length, although unity has been commonly employed in cases where length coefficients were unknown. As an alternative to this procedure I also estimated the percent fatigued at different speeds in centimeters per second and in body lengths per second for a narrow length range (10.0 to 11.9 cm total length) where the effect of differences in length would be negligible.

RESULTS

Within a few minutes after *Trachurus* were placed in the swimming compartment they became quiescent, swam steadily, and remained in about the same position in the compartment throughout the test or until they became fatigued and fell against the rear screen. This was in contrast to some other species which did not swim steadily, but swerved and oscillated from side to side.

The relationship between water speed and percent fatigue had the normal sigmoid form of a dosage response curve (Finney, 1952). Probit estimate of the applied water speed at which 50% fatigue occurred in 360 min of swimming and the 95% confidence limits were 94.40 ± 5.15 cm/sec for *Trachurus* 10.0 to 11.9 cm total length, $N = 127$ (Figure 1, Table 1). Thus, 50% of *Trachurus* in this length range could be expected to sustain a speed of about 8.4 L/sec or 22.1 $L^{0.6}$/sec for 360 min. For all *Trachurus* ($N = 294$) the water speed at which 50% fatigue occurred after 360 min of continuous swimming and the 95% confidence intervals were 22.4 ± 1.2 $L^{0.6}$/sec. The first estimate, based on a narrow length range, and the second one, based on all data, were reasonably close. On the other hand, when all data were in the form $V/L^{1.0}$ the 50% threshold was 9.34 L/sec which is higher than the preceding estimates. Inspection of these data, however, showed that the coefficient for length clearly was less than one and that use of unity biased the estimate.

TABLE 1.—Swimming endurance of *Trachurus symmetricus* in cm/sec and in $L^{0.6}$/sec.

Length 10.0-11.9 cm					Length 9.0-17.6 cm		
Speed cm/sec	N	Percent fatigued	Length		Speed[1] $L^{0.6}$/sec	N	Percent fatigued
			Mean	SD			
71	8	0	10.69	0.61	15.9	3	0
78	16	13	10.71	0.47	16.9	10	0
85	16	31	10.84	0.67	17.8	14	0
92	14	50	10.97	0.54	18.7	17	6
99	21	62	11.23	0.43	19.7	18	17
106	21	76	10.85	0.56	20.6	23	39
113	15	100	11.41	0.42	21.5	39	31
120	8	100	11.27	0.45	22.5	42	67
138	8	100	11.20	0.51	23.4	19	58
Total	127				24.3	20	60
					25.3	29	72
					26.2	19	100
					27.2	9	100
					28.1	4	100
					29.0	3	100
					30.0	1	100
					30.9	3	100
					31.8	7	100
					32.8	10	100
					33.7	4	100
					Total	294	

[1] Total speed range divided into 20 equal intervals; speeds listed are midpoints of those intervals.

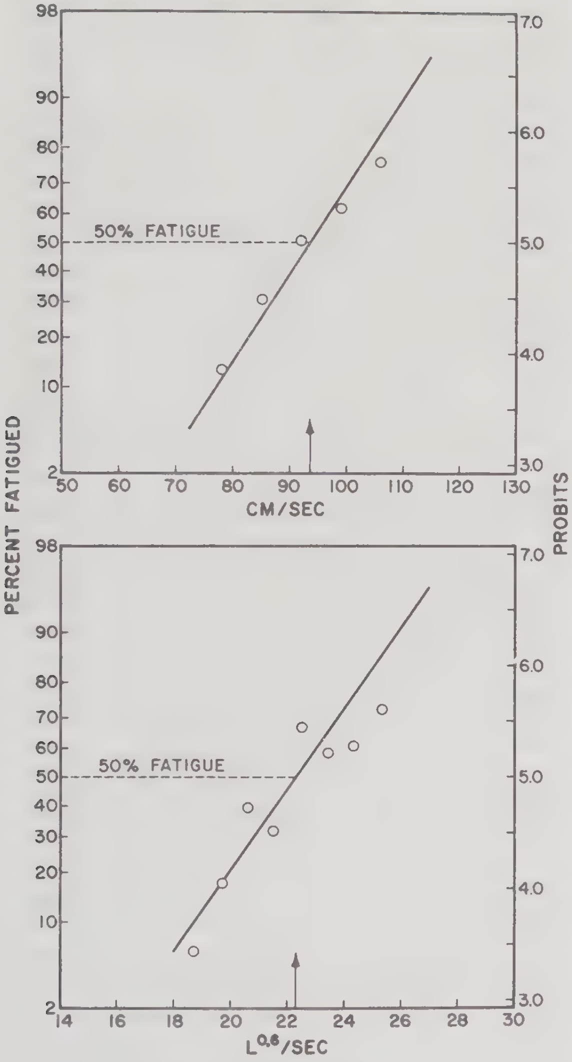

FIGURE 1.—Probit lines for sustained speed threshold for 6 hr of forced swimming at 18.5° C in juvenile *Trachurus symmetricus*. Upper panel, range fish length 10.0 to 11.9 cm $N = 127$, probit $= 0.077X - 2.238$; lower panel, range fish length 9.0 to 17.6 cm, $N = 294$, speed expressed in $L^{0.6}$/sec where L is the total length of the fish, probit $= 0.355X - 2.958$.

To determine the form of the relationship between the duration of the swimming period and the ability to maintain a certain speed, probit estimates of speed for five levels of fatigue were made for swimming periods varying from 10 to 360 min. The form of the relationship was about the same for all fatigue levels; speed estimates declined exponentially with time for short swimming periods and linearly with time for longer ones (Figure 2). The point of inflection from the exponential to the linear relationship was examined in detail for the 50% fatigue level. Probit estimates of the speed at which 50% of the fish fatigued were made for 2-min intervals of swimming cumulated over the first 100 min of observation. The data were plotted on semilog paper and a line fit by eye to the exponential function. The point of inflection appears to occur at about 22 min (Figure 3). Thus, speed at which 50% fatigued and the duration of the swimming period were exponentially related for durations up to about 22 min and were linearly related for longer periods of swimming.

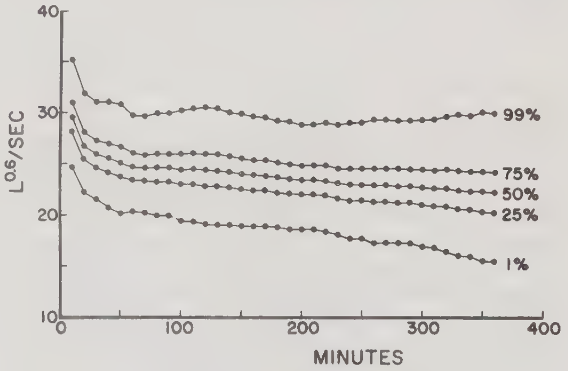

FIGURE 2.—Relation between speed in $L^{0.6}$/sec and the time it can be sustained for 1, 25, 50, 75, and 99 percent fatigue levels in *Trachurus symmetricus*. Estimates of speed for each fatigue level made at 10-min intervals of cumulated time.

The performance of juvenile *Trachurus* at high speed was of interest. Fifteen fish 14.6 cm mean total length (range = 13.4 to 16.6 cm) swam at the highest speed used in the study (160 cm/sec) for 2 to 6 min, mean time 3.4 min. Thus, *Trachurus* 15 cm total length were able to swim for about 3 min at about 10 L/sec or about 32 $L^{0.6}$/sec. A slightly higher level of

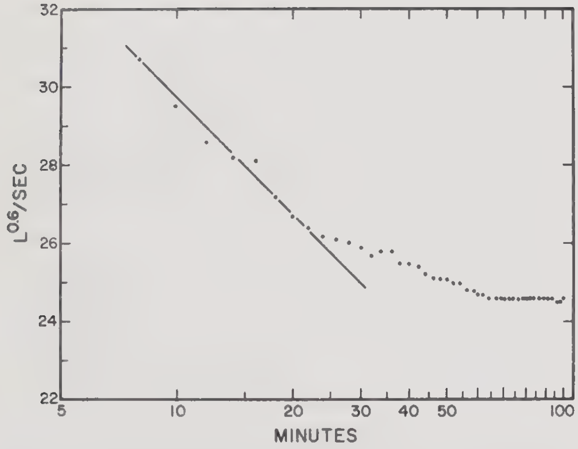

FIGURE 3.—Relation between speed at which 50% *Trachurus* fatigued and the duration of the swimming period. Duration of swimming period in minutes plotted on log scale to show exponential trend; line fit by eye. Speed estimates made at 2-min intervals of cumulated time over the first 100 min of swimming.

performance in length per second is obtained if we consider smaller fish. For example, fish of mean length 11.2 cm (length range 10.4 to 11.9 cm, $N = 8$) swam for 3 to 5 min (mean = 4.5 min) at 139 cm/sec or about 12 *L*/sec. This difference between large and small fish becomes negligible if 0.6 is used as a coefficient of length instead of unity because, as was pointed out previously, the length coefficient for *Trachurus* appears to be less than 1.

DISCUSSION

The exponential decline in swimming speed with time in fish is well documented; see for example Bainbridge (1960), Brett (1967), and Blaxter (1969). The general form of the relation between time and swimming speed in other fish resembles that for *Trachurus* although the speeds and endurance times are different in *Trachurus*. The physiological mechanisms responsible for the exponential relationship between swimming speed and endurance are generally believed to be the limited enery stores in the muscle, the rate these stores can be replaced and the rate catabolites are removed from the muscle (Bainbridge, 1960). A study by Pritchard, Hunter, and Lasker (1971) in this issue has provided an explanation for the form of the speed-time relationship in *Trachurus*. Pritchard et al. found that at speeds where an exponential relationship exists between time and speed the principal cause of failure of *Trachurus* was most likely the depletion of glycogen in the white muscle. On the other hand, fish that failed at speeds near the 6-hr 50% threshold, where a linear relationship exists between speed and time, had depleted not only the glycogen in the white muscle but that in the red muscle and liver as well. Thus, in *Trachurus* the form of the time-speed relationship could be explained on the basis of the extent of glycogen reserves available for locomotion and the time required to mobilize them from sites other than the white muscle. An exponential relationship between speed and time could be produced when the speeds are so high that the glycogen supply would be limited almost entirely to the white muscle because the supply in the white muscle would be used up and the fish would fail before significant amounts of glycogen could be mobilized from other sources. A linear relationship could exist where swimming speeds are sufficiently low that reserves in the white muscle could not be depleted before other sources in the red muscle and the liver are mobilized. We have, on one hand, a high rate of consumption using a more limited supply of fuel which could lead to an exponential relationship between speed and time and, on the other hand, a much lower rate of consumption using a relatively much larger fuel supply which could produce a linear relationship with time. An exponential relationship between energy consumption and swimming speed would enhance these effects.

Let us now consider the significance of the 6-hr sustained speed threshold determined for *Trachurus*. When compared with other determinations, this threshold appears to be unique because of different physiological mechanisms and because it is higher than those estimated for other fish. *Trachurus* at threshold speed appeared to use glycogen as fuel, white muscle for locomotion and maintained a high lactic acid level in the muscle (Pritchard et al., 1971). These results are inconsistent with the conclusion that at sustained cruising speeds, fish use lipid metabolism to drive red muscle (Bone, 1966; Gordon, 1968; Blaxter, 1969) and that no oxygen debt is incurred (Brett, 1963). Reliance on glycogen as the principal fuel probably severely limits the time a speed can be maintained as compared with one where lipid metabolism is used exclusively. Thus the biochemical evidence indicates that the 6-hr speed threshold for *Trachurus* probably could be maintained only for a period of hours or perhaps days but certainly not weeks as one would expect if fat were used as fuel. The 6-hr threshold was also considerably above sustained speed thresholds for other fish where presumably fat may be employed as fuel. Brett (1967), in a study directly comparable with the current one, found the 50% fatigue time for sockeye salmon was 4 L/sec (about 11.3 $L^{0.6}$) whereas for comparable size jack mackerel it would be about 7.6 L/sec or 22.0 $L^{0.6}$. Other less comparable data give sustained or cruising speeds in the range of 3 to 4 L/sec (Blaxter, 1969). Thus, *Trachurus* has special physiological and structural adaptations that permit swimming for periods of hours at elevated speeds and it was the threshold for this swimming behavior that was measured. Other fishes, especially the scombroid fishes, may have similar abilities. For example, skipjack tuna can swim at 8 knots, or about 43 $L^{0.6}$, for over an hour (Commercial Fisheries Review, 1969) and yellowfin tuna and skipjack tuna have higher levels of white muscle glycogen than many other species of fish (Barrett and Connor, 1964).

It seems possible another speed threshold may exist for *Trachurus* below the present one where fat is the principal fuel, only red muscle is used for locomotion, and swimming can be maintained almost indefinitely. It would not be surprising if this lower threshold were closer to those determined for other fishes.

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SWIMMING SPEED, TAIL BEAT FREQUENCY, TAIL BEAT AMPLITUDE, AND SIZE IN JACK MACKEREL, *Trachurus symmetricus,* AND OTHER FISHES

JOHN R. HUNTER AND JAMES R. ZWEIFEL[1]

ABSTRACT

The tail beat frequency and tail beat amplitude of jack mackerel, *Trachurus symmetricus*, 4.5 to 27.7 cm were measured at speeds of 15 to 212 cm/sec. Tail beat amplitude was a constant proportion of length at all speeds but tail beat frequency changed with speed; thus speed depended only on frequency of the tail beat and length. A simple mathematical model for estimating swimming speed from tail beat frequency and fish length was derived from the *Trachurus* data and applied to data for three marine fish — *Scomber japonicus, Triakis henlei,* and *Sardinops sagax* — and to data for freshwater fish from the literature. The general form of the model was $V - V_0 = L(KF - F_0)$ where V is fish speed, V_0 is length-dependent minimum swimming speed at minimum tail beat frequency F_0, and L is fish total length. The model represented a major improvement over previous equations because it provided an unbiased correction for length, was sensitive to specific differences, and provided a more accurate estimation of speed.

Of the variables that determine the swimming speed of a fish, the size of the fish, the frequency of the tail beat, and the amplitude of the tail beat are among the most important. Knowledge of the relationships between swimming speed and these variables is important not only for an understanding of the mechanism of locomotion in fish but because it may be used to forecast maximum swimming speeds (Bainbridge, 1958), to estimate swimming speeds indirectly by analysis of tail beat frequencies, and possibly to estimate fish size and make specific identifications of fish targets with doppler Continuous Transmission Frequency Modulated sonar (Hester, 1967).

Bainbridge (1958) described the relationship between tail beat frequency, tail beat amplitude, and size for three species of freshwater fish: dace, *Leuciscus leuciscus*; trout, *Salmo gairdneri* (*S. irideus*); and goldfish, *Carassius auratus.* He concluded that the amplitude of the tail beat increased with the tail beat frequency to about 5 tail beats/sec and thereafter became constant. Speeds above 5 beats/sec were dependent only on the frequency of the tail beat and the length of the fish. The relationship between speed, frequency, and length above 5 beats/sec was nearly the same in the three species studied; consequently, he used a single equation to express this relationship for all three species. No similar study exists for marine fish although some measurements of tail beat frequency and amplitude have been made incidental to other studies. Yuen (1966) measured the tail beat frequency of skipjack tuna, *Katsuwonus pelamis,* and yellowfin tuna, *Thunnus albacares,* from cine photographs taken from the viewing port of a research vessel and Magnuson and Prescott (1966) measured the tail beat frequency of Pacific bonito, *Sarda chiliensis,* from cine photographs taken through a window in an oceanarium. The slopes of the lines relating tail beat frequency to speed in body lengths per second for skipjack and yellowfin tunas and bonito were sufficiently different from those of Bainbridge (1958), for Hester (1967) to speculate that species might be identifiable by this relationship. The measurements were taken from lateral photographs of free-swimming schools; thus the tail beat amplitude and the absolute

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size of the fish were not measured and tail beat frequency was measured over a limited speed range. Fierstine and Walters (1968) measured both tail beat frequency and amplitude of wavyback skipjack, *Euthynnus affinis*, from dorsal cine photographs of free-swimming fish in circular swimming pools but only five, one-beat sequences of swimming were analyzed.

The objective of the present study was to determine the relationships between swimming speed, fish length, tail beat amplitude, and tail beat frequency in a pelagic marine fish, jack mackerel, *Trachurus symmetricus*. To accomplish this objective, dorsal cine photographs were taken of fish swimming in currents of different speeds in a specially designed activity chamber. For comparative purposes tests were also run on three other marine fish: chub mackerel, *Scomber japonicus;* Pacific sardine, *Sardinops sagax*; and a shark, *Triakis henlei.*

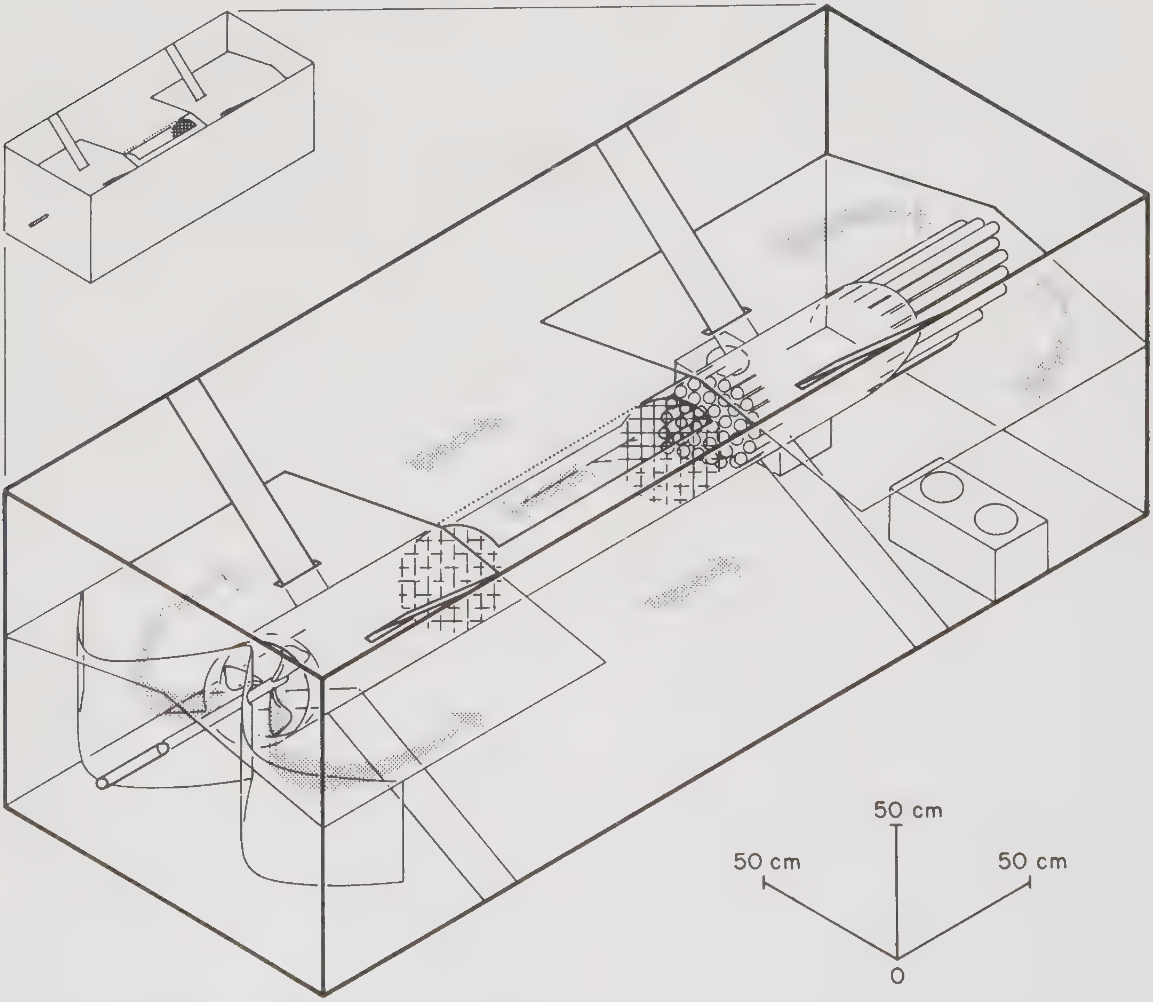

FIGURE 1.—Apparatus used to measure swimming speeds of fishes. Inset upper left apparatus shown with opaque walls; center, isometric, three dimensional scale drawing, walls, deflectors and other structures are shown as transparent for purposes of illustration; arrows indicate direction of current flow; and lower right, scale for vertical and horizontal planes of drawing.

APPARATUS

Swimming speeds were measured in an activity chamber (Figure 1) built after that of Beamish (1966). A fiber glass tube 230 cm long and 41 cm in diameter was immersed in an open bath. An 80-cm section of tube was the swimming compartment. The compartment had metal screens at the ends and a transparent acrylic plastic hatch which conformed to the contours of the tube. The walls of the tube within the swimming compartment were white and had black stripes spaced at 5.0-cm intervals to provide a visual reference for the swimming fish. Water velocity in the chamber was regulated by the speed of a 39-cm propeller driven by a variable speed 50-hp motor and by changing the screens at the two ends of the swimming compartment. Water was drawn into the compartment from the bath over deflectors, and through baffles and screens. The screens, baffles, and deflectors reduced turbulence and provided water of relatively uniform velocity throughout the swimming compartment. Their arrangement and design were determined empirically by measurement of the horizontal and vertical distribution of flow in the chamber.

The speed range of the apparatus was 12 to 212 cm/sec. The full range was obtained by changing the screens at the ends of the swimming compartment. A velocity range of 12 to 69 cm/sec was obtained when screens of 39% open area were used, one of 15 to 139 cm/sec for screens of 56% open area, and one of 19 to 212 cm/sec for screens of 75% open area.

A digital voltmeter measured to the nearest millivolt the voltage produced by a voltage generator attached to the propeller shaft. The voltage produced by the generator was proportional to propeller revolutions and was used to regulate them. An impeller flowmeter (Marine Advisers Inc., Model B-7C)[2] was used to relate propeller revolutions in volts to water flow in the apparatus. The meter sampled an area 7.6 cm in diameter and had an accuracy of ± 2.5 cm/sec when moved through static water at a known speed (for a description of the meter and a calibration curve see Olson, 1967).

Propeller revolution was related to water speed in the chamber by three series of calibrations, one for each of three screen types used. Nine to 19 different speed levels were measured in each series of calibrations. More levels were required for slow speed ranges than for fast ones because the response of the flowmeter was nonlinear at low speeds. At each level water speed was measured at 12 different radial positions midway in the swimming compartment. The speed of the water at a given level was the average of the 12 measurements, adjusted for the extent of the area sampled by the meter (Tranter and Smith, 1968). Variation among the 12 sampling points did not exceed ±10% of the mean speed and was usually much lower. The relationship between mean water speed in the chamber and propeller revolutions was linear, and the error in estimating the mean water speed from revolutions did not exceed ± 0.2 cm/sec. Thus, the principal sources of error in estimating the speed of the water in which a fish swam were the possible 10% variability in flow within the chamber and the ± 2.5 cm/sec accuracy of the flowmeter.

Fish swimming in the compartment were assumed to be swimming at the mean speed of the water in the compartment. They were photographed from above with a 16 mm high-speed motion picture camera at speeds of 64 to 200 fps. Camera speed was adjusted to provide about 10 frames per complete tail beat. A viewing box floated on the water surface above the swimming compartment to eliminate distortion in the photographs caused by ripples.

METHODS

Film was analyzed by use of a coordinate reader and digitizer (Hunter, 1966) and a computer program was used to calculate tail beat frequency and tail beat amplitude from the digitized information. One tail beat was one complete oscillation of the tail, and the tail beat frequency was the number of beats per second. Tail beat amplitude was the distance in centimeters between the lateral most excursion of the tip of the tail measured perpendicular to the axis of progression plus the mirror image of that measurement on the other side of the axis of progression.

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[2] Reference to commercial products does not imply endorsement.

The film sequences selected for analysis were usually ones in which the fish held a constant position in the current and swam steadily. Occasionally at higher speeds it was not possible to obtain such a sequence because the fish did not maintain a constant position but rather accelerated and decelerated. In this case a sequence was chosen in which no net movement existed between the beginning and end of the sequence although the fish moved slightly forward and backward within the sequence. Usually 5 complete tail beats were analyzed per speed level but occasionally as few as 2.5 and as many as 11 were analyzed.

Sixteen speed levels were used in the experiments; seven of the levels, 15 to 60 cm/sec, were graduated at intervals of 25% of the preceding level and nine of the levels, 69 to 212 cm/sec were graduated at intervals of 15%. A speed level interval greater than 10% was used because of the possible 10% variability in flow within the swimming compartment.

A grand total of 176 speed tests was analyzed for 14 jack mackerel, varying in total length from 4.5 to 27.7 cm. Owing to the differences in length, no fish was able to swim at all levels. All 14 fish swam at five levels, 24, 30, 38, 48, and 60 cm/sec, and all but the two smallest fish swam at the next five higher levels, 79, 91, 105, 121, and 139 cm/sec. Only fish of 16 cm or larger were tested at speeds above 139 cm/sec and only those less than 16 cm were tested at 15 cm/sec.

Other species were tested for comparative purposes but fewer observations were made. Seventy-four swimming sequences of five *Scomber*, 26.3 to 32.2 cm total length, were analyzed, nine sequences of five *Sardinops*, average length 13.6 cm, and seven sequences of one *Triakis*, 23.6 cm.

All fish were tested singly except for *Sardinops*, which was tested in a group of five. Fish were held in the swimming compartment at a low speed for about 30 min before an experiment began. Seawater temperature ranged from 17.0° to 19.5° C among experiments but did not vary over a degree within an experiment.

RESULTS

The tail beat amplitude of *Trachurus* did not change with speed but was constant at all speed levels and was directly related to length (Figures 2 and 3). Tail beat frequency, on the other hand, changed with speed and, therefore, was the only speed modulator measured in these experiments. In all species studied the relationship between tail beat frequency and velocity

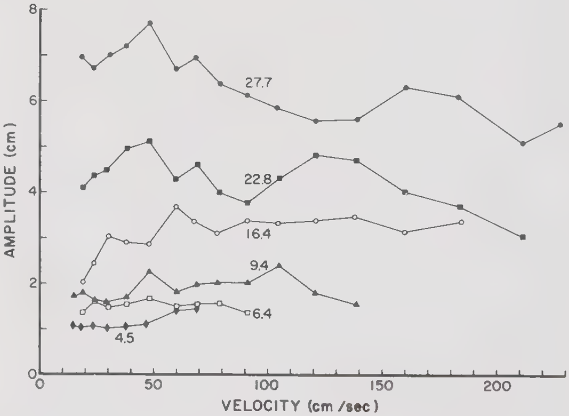

FIGURE 2.—Tail beat amplitude at various speeds for six *Trachurus*, 4.5 to 27.7 cm total length.

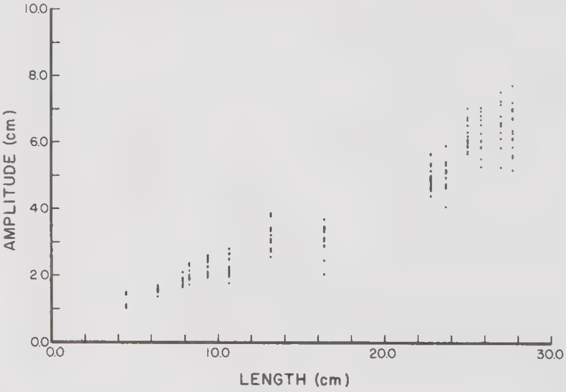

FIGURE 3.—Relationship between tail beat amplitude and total length for 14 *Trachurus*, 4.5 to 27.7 cm total length. ($A = 0.23177L$, $s_{yx} = 5.068$, and $N = 176$.)

was linear throughout the range of test speeds, but the slope and intercept of the regression lines varied with fish length (Figure 4, Table 1).

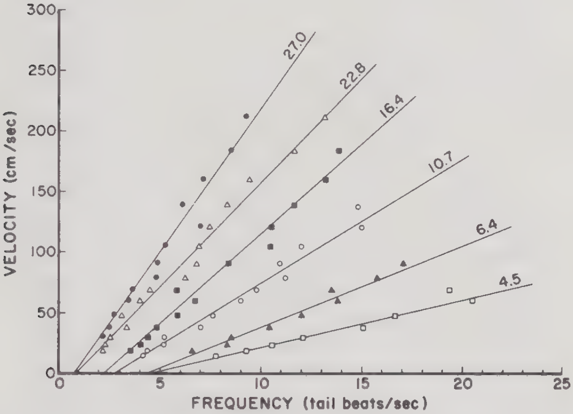

FIGURE 4.—Relationship between speed and tail beat frequency for six *Trachurus*, 4.5 to 27.0 cm total length. Equations for regression lines shown in figure are given in Table 1.

TABLE 1.—Standard deviation (s_{yx}), intercept (a), and slope (b) for regression of speed (cm/sec) on tail beat frequency and slope and intercept for regression of speed/length on frequency for *Trachurus*.

Length (cm)	N	Speed (cm/sec) on frequency			Speed/length on frequency	
		a	b	s_{yx}	a	b
4.5	8	—17.786	3.996	3.889	—3.952	0.888
6.4	9	—29.761	6.838	4.284	—4.650	1.068
7.9	11	—37.527	8.326	4.135	—4.624	1.054
8.3	11	—39.736	9.374	10.096	—4.787	1.129
9.4	13	—35.241	8.953	5.258	—3.749	0.952
10.7	13	—29.012	10.431	5.612	—2.781	0.975
13.2	13	—19.860	11.514	10.762	—1.504	0.873
16.4	14	—32.541	14.780	9.060	—1.984	0.901
22.8	15	—15.407	17.497	6.945	—0.676	0.767
23.7	13	—13.723	19.753	6.457	—0.579	0.833
25.0	15	—33.403	23.394	11.832	—1.336	0.936
25.8	13	—23.220	21.730	8.734	—0.900	0.842
27.0	13	—20.521	23.960	9.157	—0.760	0.887
27.7	15	—11.240	20.509	9.182	—0.406	0.740
Total	176					

The length-dependent differences in intercept were probably a function of differences in minimum speed and minimum tail beat frequency. Fish have a minimum tail beat frequency and a minimum swimming speed below which they cannot swim by movement of the caudal fin and these minima were a function of body length. In the past, speed was scaled directly to length; that is, speed was divided by length and regressed on frequency (Bainbridge, 1958; Magnuson and Prescott, 1966; Yuen, 1966). Our data suggest, however, that division of speed by length would introduce bias because of the existence of a minimum speed and tail beat frequency different from zero, the dependence of minimum speed on length, and possible length-dependent differences in the slope of the regression of speed on frequency. For example, when we divided speed by length, size-dependent differences in intercept and possibly the slope still existed (Table 1, last two columns). In addition a curvilinear trend is introduced at low speeds in the combined data because of the lack of an intercept (minimum speed) correction. Thus an equation that relates speed to tail beat frequency for fish of different length must include an adjustment for size-dependent differences in minimum swimming speed, minimum tail beat frequency, and perhaps also for size-dependent differences in the slope coefficient.

The existence of size-dependent variables introduces certain problems in the interpretation of these data because of the possibility that specific differences in size dependency may exist. For example, differences exist among species in the coefficients used to relate size to various swimming characteristics such as burst and sustained speeds (Bainbridge, 1960) but it is uncertain whether or not these differences reflect real specific differences or if they are simply differing estimates of a common coefficient. Owing to the great variability inherent in swimming speed studies and because of the sensitivity of the length coefficients to the size range of animals in the sample, these two alternatives are equally plausible. In addition, specific differences in the relationship between size and swimming functions may also depend on the particular function considered (Bainbridge, 1960). For example, the coefficient relating size to maximum sustained speed may be different from the one that relates size to beat frequency or burst speed. Thus, species may differ from one another in the way each swimming function is related to size. If such specific differences exist then direct comparisons between species are impossible, but if they do not exist then a general model can be derived from our data which can be used to make specific comparisons. In the interpretation of our data on *Trachurus* we will consider the alternatives, Case I where all swimming functions are related to size on a species-specific basis, and Case II where swimming functions are proportional to the same power of length in different species.

To evaluate Case I where length coefficients are considered to be species-specific we regressed speed on frequency by the general relationship.

$$V = \alpha_1 L^{\alpha_2} + \alpha_3 L^{\alpha_4} * F$$

where V is swimming speed in centimeters per second, F is tail beat frequency in beats per second, L is total length in centimeters and $\alpha_1 L^{\alpha_2}$ is the intercept function and $\alpha_3 L^{\alpha_4}$ is the slope function for the tail beat frequency-swimming speed relationship. Estimates were obtained by use of Marquardt's Algorithm for fitting nonlinear models (Conway, Glass, and Wilcox, 1970). For *Trachurus* the 90% support-plane confidence intervals (Conway et al., 1970) for α_3 and α_4 were $0.72 < \alpha_3 < 1.82$ and $0.72 < \alpha_4 < 1.01$ where $\hat{\alpha}_3 = 1.28$ and $\hat{\alpha}_4 = 0.86$.

To evaluate Case II where length coefficients are the same for all fish we assumed the slope coefficient α_4 equaled one. When $\alpha_4 = 1$, $\hat{\alpha}_3 = 0.86$ with 90% confidence limits of $0.79 < \alpha_3 < 0.91$. On the basis of the *Trachurus* data alone there seems to be little or no difference between the use of unity for the slope coefficient or use of the estimated value of 0.86. The similarity in the two estimates is apparent when the actual fish lengths are substituted into the two equations and the two sets of slopes are compared (Table 2, columns 1 and 2).

We fitted the Case I model to four additional species to determine the extent they differed in the length coefficient for the slope in the speed-tail beat frequency relationship. Used in this comparison were data we collected on *Scomber*, and data presented in scatter plots of velocity and frequency for individual *Carassius*, *Salmo*, and *Leuciscus* by Bainbridge (1958). We used the *XY* digitizer to transcribe Bainbridge's data onto cards. We may have failed to interpret correctly some of the overlapped points in his graphs but the effect of these errors on the statistical parameters we estimated would be negligible. We did not use the data presented by Magnuson and Prescott (1966), Yuen (1966), or Fierstine and Walters (1968) because in these studies the absolute speeds and the lengths of the fish were unknown.

Our estimates of the slope coefficient for the speed-tail beat relationship, $\hat{\alpha}_4$, varied from 0.76 in *Salmo* to 1.22 in *Carassius*, and the 90%

TABLE 2.—Slopes for the speed-frequency relationship for individual *Trachurus* when the general relationship is slope $= 1.28\ L^{0.86}$ (Case I) and when slope $= 0.86L$ (Case II); estimated minimum speed (V_0) for each fish when $V_0 = 0.80L^{2/3}$; lowest observed test speed (V_{obs}); the minimum tail beat frequency (F_0) estimated by substitution of V_0 the Case II equation for each fish; and the lowest observed tail beat frequency (F_{obs}).

Length (cm)	$b = 1.28L^{0.86}$ Case I	$b = 0.86L$ Case II	$V_0 = 0.80L^{2/3}$	V_{obs}	$F_0 = 3.98L^{-1/3}$ Case II	F_{obs}
4.5	4.67	3.87	2.19	14.9	2.41	7.77
6.4	6.32	5.50	2.77	18.9	2.14	6.60
7.9	7.57	6.79	3.19	24.0	2.00	6.75
8.3	7.90	7.14	3.30	24.0	1.97	6.68
9.4	8.79	8.08	3.59	15.1	1.88	5.22
10.7	9.83	9.20	3.92	15.0	1.81	4.18
13.2	10.98	11.35	4.51	15.0	1.68	2.91
16.4	14.19	14.10	5.21	19.0	1.56	3.56
22.8	18.84	19.61	6.50	18.9	1.40	2.18
23.7	19.48	20.38	6.67	24.1	1.38	1.86
25.0	20.39	21.50	6.91	19.8	1.36	2.46
25.8	20.95	22.19	7.06	24.7	1.35	2.11
27.0	21.78	23.22	7.28	31.4	1.33	2.16
27.7	22.27	23.82	7.40	19.0	1.32	1.78

support-plane intervals for $\hat{\alpha}_4$ in all species included unity (Table 3). Clearly if a common slope-length coefficient exists among these species, it must be close to 1. We conclude the assumption of unity for the slope-length coefficient is an acceptable practice and that it appears to introduce no significant bias in the species studied.

We now turn to the problem of estimation of the length-dependent coefficient for the intercept of the speed-tail beat relationship, that is, α_2. We noted previously that the biological significance of the existence of an intercept different from zero in the speed-frequency relationship may be that fish have a minimum speed below which they cannot swim by movements of the caudal fin. If we assume that the intercept is a function of the minimum swimming speed of a fish we can make an independent estimate of the intercept coefficient using an equation derived by Magnuson (1970) for estimation of the minimum swimming speed (V_0) of *E. affinis.* A somewhat simplified form of his equation is:

$$V_0 = \left(1 - \frac{D_e}{D_f} \right)^{1/2} * \left[\frac{g * Ma}{(C_{lf}A_{ft}) * \frac{p}{2}} \right]^{1/2}$$

where D_e is 1.025 (the density of sea water), D_f is the density of the fish, g is 980 cm/sec (the acceleration of gravity), Ma is mass of fish in air, C_{lf} is the coefficient of lift for the pectorals (assumed to equal 1), A_{ft} is the total lifting area of the extended pectoral fins in square centimeters, and p is the density of sea water, 1.025 g/cc. If we let $Ma = 0.004407 L^{3.21215}$ (the length-weight relationship for *T. symmetricus*, $N = 264$, unpublished data, Na-

TABLE 3.—Estimates of length coefficients for slope and intercept for five species of fish.

Species	$V = \alpha_1 L^{\alpha_2} + \alpha_3 L^{\alpha_4} * F$	90% support-plane interval[1]
Trachuhus symmetricus	$V = -44.57L^{-0.24} + 1.28L^{0.86} * F$	$-111.18 < \alpha_1 < 22.65$ $-0.80 < \alpha_2 < 0.31$ $0.73 < \alpha_3 < 1.82$ $0.72 < \alpha_4 < 1.01$ $s_{vf} = 11.41$
Scomber japonicus	$V = -0.56L^{0.55} + 1.20L^{0.83} * F$	$-160.78 < \alpha_1 < 159.66$ $-84.14 < \alpha_2 < 85.25$ $-8.15 < \alpha_3 < 10.57$ $-1.46 < \alpha_4 < 3.13$ $s_{vf} = 21.42$
Leuciscus leuciscus[2]	$V = -3.36L^{0.40} + 0.80L^{0.98} * F$	$-14.95 < \alpha_1 < 8.24$ $-0.84 < \alpha_2 < 1.65$ $0.47 < \alpha_3 < 1.12$ $0.85 < \alpha_4 < 1.12$ $s_{vf} = 7.81$
Salmo gairdneri[2]	$V = -1.77L^{0.64} + 1.40L^{0.76} * F$	$-14.79 < \alpha_1 < 11.26$ $-0.70 < \alpha_2 < 2.97$ $0.33 < \alpha_3 < 2.46$ $0.52 < \alpha_4 < 1.00$ $s_{vf} = 14.16$
Carassius auratus[2]	$V = -0.12L^{1.52} + 0.40L^{1.22} * F$	$-0.89 < \alpha_1 < 0.64$ $-0.50 < \alpha_2 < 3.53$ $0.17 < \alpha_3 < 0.63$ $1.01 < \alpha_4 < 1.44$ $s_{vf} = 5.54$

[1] Simultaneous confidence intervals for all parameters (Conway, Glass, and Wilcox, 1970).
[2] Data from Bainbridge (1958).

tional Marine Fisheries Service, La Jolla, Calif.), Area $= 0.02811L^{1.9124}$ (lifting area of pectorals of *T. symmetricus* was equal to twice the pectoral fin area), and $D_f = 1.03$ (the density of *T. trachurus* from Alexander (1959b), a closely related species to *T. symmetricus*), we obtain an estimate of $V_0 = 0.86L^{0.65}$ for *Trachurus.* This value is considerably below $10L^{0.50}$ obtained for *Euthynnus* by Magnuson (1970). The minimum swimming speed of *Trachurus* would be expected to be lower than that of *Euthynnus* because *Euthynnus* lacks a swim bladder and has a high specific gravity. Indeed, the minimum speed of *Euthynnus* is close to the endurance speed of many fishes with swim bladders (Magnuson, 1970).

In all other species except *Carassius* estimation of minimum speed was not possible because we had few or no estimates of the variables required in Magnuson's equation. In *Carassius* we used the specific gravity for carp, 1.002 g/cc (Alexander, 1959a), the pectoral fin area relationship of Area $= 0.02811L^{1.9124}$ from data we collected on seven *Carassius* 4.6 to 22.5 cm total length (the lifting area of the pectorals equaled twice the pectoral fin area) and the length-weight relationship of $Ma = 0.0065L^{3.20}$ for the seven *Carassius.* The estimate of minimum swimming speed V_0 for *Carassius* from these data was $0.87L^{0.65}$. This estimate was nearly the same as the one estimated above for *Trachurus* and it had the same coefficient of length. Thus, in *Trachurus* and in *Carassius* the minimum speed coefficient of length or, in our equation, the intercept coefficient $\hat{\alpha}_2$, was 0.65.

That the length coefficient for the intercept was the same in *Carassius* and *Trachurus* supports the basic assumption of the Case II model, that is, the existence of common length coefficient among different species. To further test this assumption we estimated the intercept coefficient by fitting the combined data from all five species listed in Table 3 to the reduced Case II model

$$V = \alpha_1 L^{\alpha_2} + \alpha_3 L * F$$

The estimate α_2 for the combined data was 0.68 with 90% confidence limits of $-0.56 < \alpha_2 < 1.92$. Although the limits were wide, the estimate was very close to the other independent estimate for *Carassius* and *Trachurus* and suggests that the true value may be close to 2/3.

The evidence we presented supported the use of the Case II equation and the use of 2/3 for the length-dependent coefficient for the intercept function and of unity for the length-dependent coefficient of the slope function. Thus, we fit the reduced Case II model

$$V = \alpha_1 L^{2/3} + \alpha_2 L * F$$

to the data from each of the five species listed in Table 3 and to that from two additional species *Triakis* and *Sardinops* for which we had a small number of observations. The resultant equations were useful nonbiased predictive models for the estimation of speed (V) from length (L) and tail beat frequency (F) in each species (Table 4). The regression lines for these equations do not pass through the origin, however. They cut the abscissa before zero and consequently the intercept terms are negative. We pointed out previously that we believe the existence of a negative intercept in the raw data implied that the fish had a minimum swimming speed below which they cannot swim by beating only the caudal fin. Thus, to make the model more biologically meaningful we adjusted the elevation of the intercept function to correspond to the theoretical minimum swimming speed, V_0. (It should be remembered that the length-dependent slope of V_0 was about the same as the length coefficient, α_2, and it was this similarity that led us to use 2/3 as the intercept coefficient.)

To express the Case II model in terms of minimum speed we used V_0 estimated from Magnuson's equation to solve for a minimum tail beat frequency, F_0, and expressed the final relationship in the form

$$\frac{V - V_0}{L} = KF - F_0 .$$

In species other than *Trachurus* and *Carassius,* a theoretical estimate of V_0 was not possible and consequently we assumed V_0 was propor-

TABLE 4.—Swimming speed-tail beat frequency equations for seven species of fish.

Species	$V = \alpha_1 L^{2/3} + \alpha_3 L * F$	90% support-plane interval[1]
Triakis henlei	$V = -1.39L^{2/3} + 0.93L * F$	$-2.71 < \alpha_1 < -0.01$ $0.77 < \alpha_2 < 1.09$ $s_{vf} = 2.49$
Trachurus symmetricus	$V = -2.50L^{2/3} + 0.83L * F$	$-3.28 < \alpha_1 < -1.59$ $0.78 < \alpha_2 < 0.88$ $s_{vf} = 12.39$
Scomber japonicus[2]	$V = -2.20L^{2/3} + 0.82L * F$	$-3.18 < \alpha_1 < -1.13$ $0.76 < \alpha_2 < 0.88$ $s_{vf} = 12.31$
Leuciscus leuciscus	$V = -1.58L^{2/3} + 0.74L * F$	$-2.21 < \alpha_1 < -0.86$ $0.71 < \alpha_2 < 0.78$ $s_{vf} = 7.78$
Carassius auratus	$V = -0.66L^{2/3} + 0.66L * F$	$-1.47 < \alpha_1 < 0.17$ $0.61 < \alpha_2 < 0.74$ $s_{vf} = 6.09$
Salmo gairdneri	$V = -1.28L^{2/3} + 0.64L * F$	$-2.63 < \alpha_1 < 0.13$ $0.59 < \alpha_2 < 0.69$ $s_{vf} = 17.72$
Sardinops sagax	$V = 0.49L^{2/3} + 0.50L * F$	$-1.61 < \alpha_1 < 2.58$ $0.39 < \alpha_2 < 0.62$ $s_{vf} = 5.77$

[1] Simultaneous confidence intervals for all parameters (Conway, Glass, and Wilcox, 1970).

[2] One deviant fish omitted; if fish included $V = -0.53L^{2/3} + 0.66L * F$, and $s_{vf} = 21.31$.

tional to $L^{2/3}$. The elevation of the line relating V_0 to length for a species was estimated by assuming that the lowest observed speed fell on that line. For *Trachurus* and *Carassius* we recalculated the elevation for a slope of 2/3.

Our estimates of V_0 and F_0 were not definitive. For *Trachurus* no fish were tested at speeds close to the theoretical minimum. Our estimates based on the theoretical minimum speed were closest to the observed minimum speeds in fish 9.4 cm total length and larger (Table 2) because in these larger fish the test speeds were sufficiently low for fish to swim with pectoral fins fully extended, an event that occurs near the minimum swimming speed (Magnuson, 1970). For *Carassius* the agreement between the theoretical estimate of minimum speed and observed minimum speeds was better (Table 5). The explanation for this is that the techniques used by Bainbridge (1958) permitted estimates at much lower speeds than the one we used. These data clearly show that in neither *Trachurus* (Table 2) nor *Carassius* (Table 5) was either V_0 or F_0 seriously overestimated. We feel that our estimates for these two species were reliable.

The fit to the general equation was good in all species (Figure 5, Table 6). The intercept for the regression line did not differ from zero and the scatter at low velocities was less than it was when no intercept correction was used (see figures in Bainbridge (1958) for comparison). The regression coefficient, K, in our equation differed among species. For the five species for which significant data were available, it was the highest in *Trachurus* and lowest in *Salmo*. Since amplitude was a constant, these results implied that the speed output per beat of the caudal fin was greater in *Trachurus* and *Scomber* than it was in *Salmo* and *Carassius*. In *Scomber*, the coefficient, K, may be uncertain because the values of one of the five fish tested deviated considerably from the rest. In Figure 5, all of the values to the right of the regression line above

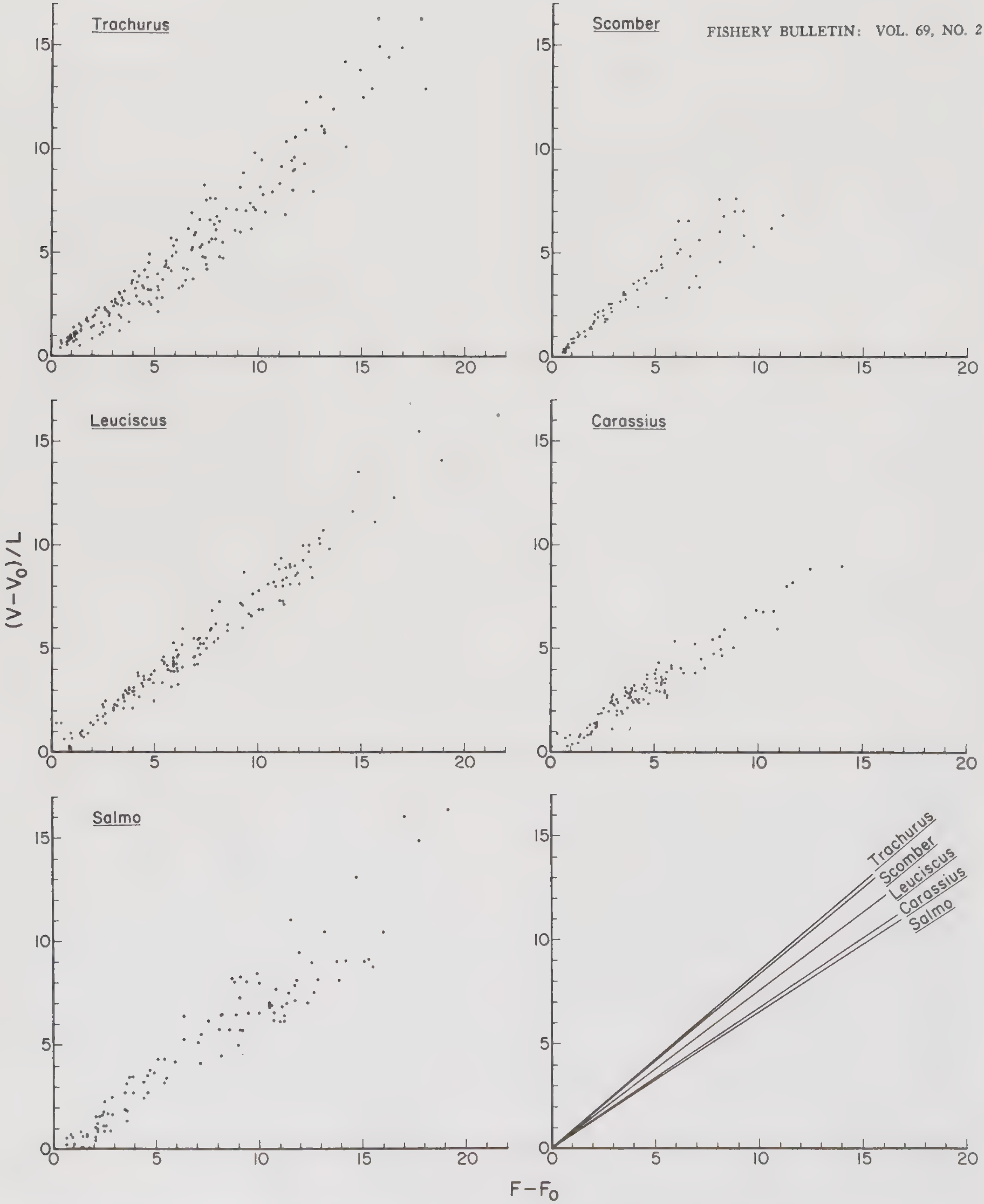

FIGURE 5.—Relationship between swimming speed corrected for minimum speed over length and tail beat frequency corrected for minimum frequency for *Trachurus* and *Scomber* from the present data, and for *Leuciscus*, *Salmo*, and *Carassius* from Bainbridge (1958). Graph at lower right shows individual regression lines for all above species, equations for lines are given in Table 6.

Table 5.—Slopes for the velocity-frequency relationship for individual *Carassius* studied by Bainbridge (1958) when the general relationship is slope $= 0.68L$; estimated minimum speed when $V_0 = 0.81L^{2/3}$; observed minimum swimming speed (V_{obs}); the tail beat frequency F_0 estimated by substitution of V_0 into the corrected slope equation; and the lowest observed tail beat frequency (F_{obs}).

Length (cm)	$b = 0.66L$	$V_0 = 0.81L^{2/3}$	[1]V_{obs}	$F_0 = 2.22L^{-1/3}$	F_{obs}
4.6	3.04	2.25	3.50	1.34	1.30
7.0	4.62	2.98	9.30	1.17	1.52
9.5	6.27	3.66	11.60	1.04	2.03
15.2	10.03	5.01	33.70	0.90	3.38
22.5	14.85	6.52	13.70	0.78	1.63

[1] Data from Bainbridge (1958).

TABLE 6.—Minimum speed (V_0), minimum tail beat frequency (F_0), the coefficient K in equation $V - V_0 = L(KF - F_0)$ arranged in order of K.

Species	N	V_0	F_0	K
Triakis henlei	6	$0.15L^{2/3}$	$1.66L^{-1/3}$	0.93
Trachurus symmetricus	176	[1]$0.80L^{2/3}$	$3.98L^{-1/3}$	0.83
Scomber japonicus	[2]61	$1.31L^{2/3}$	$3.51L^{-1/3}$	0.82
Leuciscus leuciscus[3]	149	$0.67L^{2/3}$	$3.04L^{-1/3}$	0.74
Carassius auratus[3]	111	[1]$0.81L^{2/3}$	$2.22L^{-1/3}$	0.66
Salmo gairdneri[3]	109	$0.52L^{2/3}$	$2.81L^{-1/3}$	0.64
Sardinops sagax	9	$2.23L^{2/3}$	$3.48L^{-1/3}$	0.50

[1] V_0 theoretical estimate based on equation of Magnuson (1970).
[2] One deviant fish omitted; if fish included, $N = 74$, $K = 0.66$.
[3] Original data from Bainbridge (1958).

4 beats/sec on the abscissa were from this single deviant fish. If the deviant fish is included $K = 0.66$, but if not, $K = 0.82$. We are inclined to use $K = 0.82$ because the values for the four fish were very similar and the protocol indicated that the deviant fish may have been overly fatigued when tested. *Triakis* appears to have a relatively high coefficient but not too much significance can be attached to the exact value for *Triakis* or for *Sardinops* because these were based on so few measurements.

In sum, the speed-tail beat equation (Case II) —Table 6—was biologically as well as statistically relevant, was sensitive to specific differences in swimming behavior, provided an unbiased correction for length, and made possible a more accurate estimation of swimming speed from tail beat frequency than heretofore has been possible.

TAIL BEAT AMPLITUDE

We pointed out previously that tail beat amplitude was a constant and was directly proportional to length and consequently the size coefficients for amplitude are probably the same as those for length. Thus amplitude (A) in centimeters can be substituted for length in the original Case II equation $V = \alpha_1 A^{2/3} + \alpha_3 L * F$. When this was done for *Trachurus* using all individual amplitude values ($N = 176$), we obtained the equation; $V = -6.5767A^{2/3} + 3.5637A * F$. The amplitude coefficient may be also estimated by substitution of the amplitude-length relationship for *Trachurus* ($A = 0.23177L$), into the Case II equation.

The tail beat amplitude data collected by Bainbridge (1958) were insufficient for specific estimates of an amplitude coefficient. The mean amplitudes for each of the fish we studied and for each of those studied by Bainbridge were nearly the same, when adjusted for body length. Variation within a species was as great as that between species (Figure 6). The relationship between mean tail beat amplitude and length for all species combined was $A = 0.21L$.

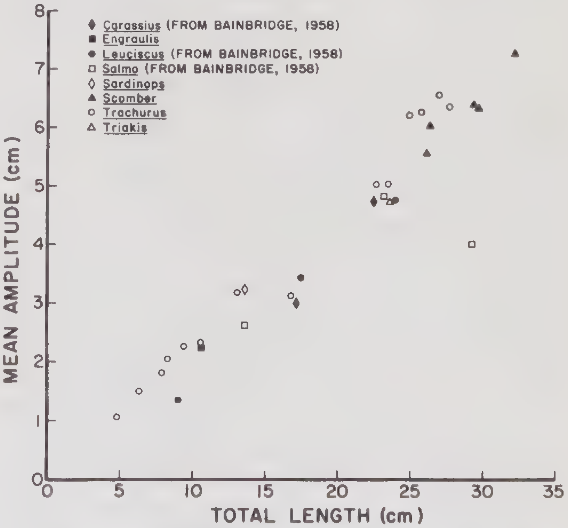

FIGURE 6.—Relationship between mean tail beat amplitude and length for every fish we studied and all those studied by Bainbridge (1958), $A = 0.21L$.

DISCUSSION

In all previous studies speed was divided by length then related to tail beat frequency. In our data when speed was converted to body lengths per second the relationship between speed and frequency was nearly identical to that given by Bainbridge (1958) for *Carassius, Leuciscus,* and *Salmo.* The confidence intervals for the slopes in the speed-frequency relationship in *Euthynnus* and *Thunnus* (Yuen, 1966) and in *Sarda* (Magnuson and Prescott, 1966) overlap the slope in the Bainbridge equation and the ones for *Trachurus* and *Scomber* when the body length conversion is used. Thus, when speed is in body lengths per second, the relationship between it and frequency is about the same in all fish studied to date from goldfish to mackerel and is adequately described by the Bainbridge equation $V/L = bf$. Thus the Bainbridge equation provides a description of the average relationship for fish in general but little significance can be attached to specific differences in slope. If more than a rough estimate of speed is required or if specific differences are important, or if estimates are needed near the minimum swimming speed it would be necessary to use the equation developed in this study.

Bainbridge (1958) concluded from his data that the frequency-speed relationship was curvilinear below a frequency of about 5 beats/sec because fish modulated their tail beat amplitude. His evidence for this conclusion was that in some fish amplitude appeared to decrease at lower frequencies, and that the distance per beat, calculated by dividing speed by frequency, declined at frequencies below 5 beats/sec but was constant above that frequency. His evidence for amplitude modulation at low speeds was weak. In the three *Salmo* studied no trend existed; in *Carassius* he suggested there might be a decrease in amplitude in one of the two fish studied, and in one of the two *Leuciscus* studied a trend existed slightly stronger than the one in *Carassius.* In sum, the evidence for a decline in amplitude measurements was based on possible trends in two of the seven fish studied. Two fish could easily give a misleading picture of the general trend in the data, especially when the variability in amplitude measurements are considered. In our studies we measured the tail beat amplitude in every fish at all possible speed levels and no evidence existed for a consistent change in amplitude with speed.

In Bainbridge's data the departure of distance traveled per beat from a constant at low frequencies was caused by the division of speed by frequency. Had the line relating frequency to speed passed through the origin, no bias would have existed but because the line intersected the abscissa at about 1 beat/sec division by frequency produced an artificial curvilinear trend at lower frequencies. We produced the same trend in distance per beat in our data by dividing speed by frequency but the trend was eliminated when a correction for the intercept was used. Thus the curvilinear trend in distance per beat in Bainbridge's data was an artifact caused by the method of calculation and consequently distance per beat was a constant at all frequencies. In addition, the apparent nonlinearity below 5 beats/sec in his graphs relating speed divided by length to frequency was also the result of the same intercept problem. Therefore, no evidence exists for consistent amplitude modulation at any speed range and speed appears to be related only to tail beat frequency and length in the species studied by Bainbridge (1958) as well as in the ones we studied. We concluded that during steady swimming at any speed, tail beat amplitude is a constant proportion of body length of the order of 0.21 *L.*

That the mean amplitude during steady swimming was constant does not mean that amplitude is not modulated under certain conditions. It is widely known that fish modulate tail beat amplitude when they accelerate (Gray, 1968). Further, we had the impression that some of the variability in the speed-frequency relationship was caused by differences in amplitude. These differences were infrequent and irregular in occurrence and consequently we were not able to evaluate them statistically. We are inclined to believe, however, that fish occasionally made minor adjustments in amplitude and frequency over the entire range of speeds, but these adjustments were merely individual deviations from the general relationship we have described.

We do not wish to detract from the original and important contribution of Bainbridge (1958), by emphasis on the differences between his and our conclusions. His basic conclusions and equations were not greatly different from our own. We were able to examine more closely the form of the relationships he described because of a larger sample size made possible by the availability of automatic film analysis equipment and because of the existence of his data in the literature.

The question of species-specific size effects remains unresolved. In our general model a good fit was obtained in seven species when the minimum stalling speed was proportional to $L^{2/3}$, the frequency at this minimum speed was proportional to $L^{-1/3}$, and the slope coefficient was proportional to $L^{1.0}$. A comparative study on speed-related size effects in fishes would certainly be of value.

It also remains to be resolved whether or not it was appropriate to apply the minimum swimming speed equation developed by Magnuson (1970) for *Euthynnus affinis*, a fish that lacks a swim bladder, to such a broad assortment of species. The equation implies a functional relationship between minimum speed and hydrostatic equilibrium and implies existence of negative buoyancy at minimum speeds. We do not know if these relationships exist in all species; nevertheless his equation did provide a reasonable estimate for minimum speed and it functioned well in our equation.

The relationship between swimming speed and tail beat frequency we have described could be used in any application where it is necessary to measure swimming speeds of fish. For example, a sonic internal tag could be developed that telemetered tail beat frequency and thus the speed of free-swimming fish could be monitored continuously over extended periods.

The tail beat frequency-speed relationship could be used for size or species identification using Continuous Transmission Frequency Modulated sonar as suggested by Hester (1967). The increase of speed with frequency (our K value) varied from species to species and thus might be used for identification. If size were known, the minimum observed velocity would provide additional information for identification. Alternatively, if the species were known, minimum (or maximum) speed would provide an indication of size. The equation could also be used to estimate size from tail beat amplitude, but caution should be exercised because in our study amplitude was not modulated and consequently, we do not know whether or not speed and tail beat amplitude are linearly related within an individual.

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Use of Threadfin Shad, Dorosoma petenense, as Live Bait During Experimental Pole-and-Line Fishing for Skipjack Tuna, Katsuwonus pelamis, in Hawaii.

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ABSTRACT

The effectiveness of threadfin shad as a live bait for skipjack tuna fishing in Hawaii was compared with the normal anchovy bait (nehu) during experimental fishing on 37 schools of skipjack tuna during 1967 and 1968 aboard the research vessel Charles H. Gilbert. Threadfin shad proved about as effective as nehu in (1) luring skipjack tuna to the stern of the vessel, (2) concentrating the skipjack tuna at the fishing station, and (3) catch rate of skipjack tuna. Underwater observations of threadfin shad and nehu indicate a general similarity in behavior during fishing. Bait-sized threadfin shad occur in freshwater impoundments in Hawaii during the peak months of skipjack tuna fishing. They are hardy, easily acclimated to salt water, and readily handled in large numbers.

INTRODUCTION

Reducing the time now required to catch live bait has been suggested as a major step to increase the fishing effort of the pole-and-line fishery for skipjack tuna, Katsuwonus pelamis, in Hawaii (Brock and Uchida, 1968; Shang, 1969). For several years, developing a new live bait which could be obtained from a bait station by Hawaiian fishermen has been a goal of the National Marine Fisheries Service, Hawaii Area Fishery Research Center.

Threadfin shad, Dorosoma petenense, is one baitfish (Figure 1) that has been extensively investigated. Any new baitfish must meet three basic requirements: It should be effective under fishing conditions, capable of mass production, and hardy. I here report on the ability of shad to fulfill one of these requirements—effectiveness during experimental pole-and-line fishing aboard a research vessel. Observations on the behavior and hardiness of bait are also included.

The fishing methods and catch statistics of the Hawaiian fishery for skipjack tuna have been described by Uchida (1967) and by Brock and Uchida (1968). The fishery produces an average catch of about 5,000 tons of skipjack tuna each year. Each vessel catches its own live bait that is taken to sea in baitwells and chummed into the water to lure skipjack to the stern of the vessel and within range of the fishermen's hooks. A small, silvery anchovy called nehu, Stolephorus purpureus (Figure 2), occurs in several bays in Hawaii and makes up 92% of the bait catch. It is a delicate fish and sometimes in short supply. Bait catching takes place during the day and night. Day baiting is a time-consuming activity, making up about 32% of the total time devoted by the boats to scouting, fishing, and day baiting. Reduction in the time spent day baiting should result in more

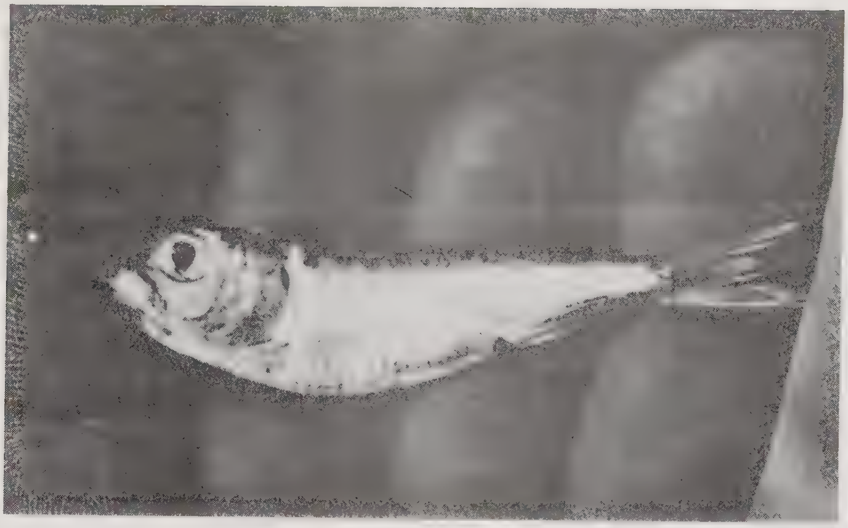

Figure 1.--Threadfin shad, Dorosoma petenense.

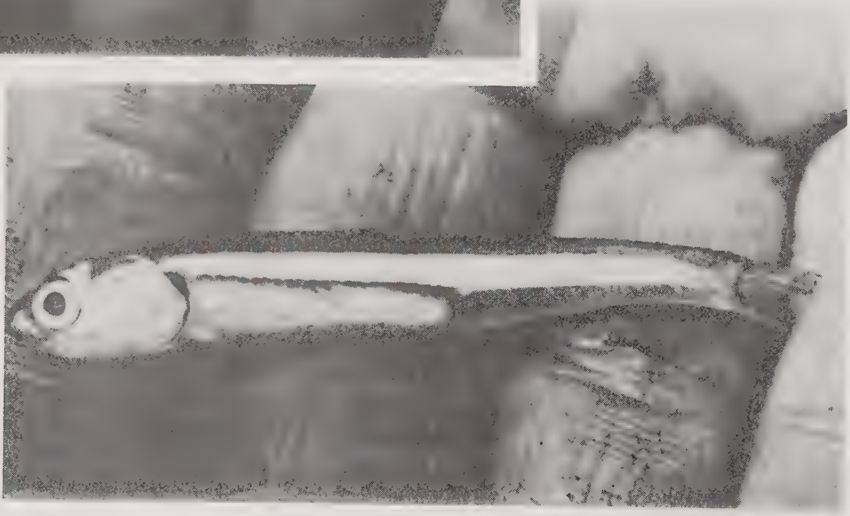

Figure 2.--Nehu, Stolephorus purpureus.

actual fishing time and should increase the overall catch of the fishermen.

Threadfin shad were first introduced into freshwater impoundments and streams in Hawaii in 1958 and by 1960 had become established in several reservoirs (Hida and Thomson, 1962). Among the attributes of threadfin shad which led to their investigation as a new baitfish are: tolerance to both salt and fresh water, hardiness, silvery color, size, swimming behavior, and low mortality during mass handling. Also, the use of threadfin shad would not require any major changes in the methods used by skipjack tuna fishermen in Hawaii. In recent years threadfin shad in Wahiawa Reservoir, Oahu, have become sufficiently abundant to make large-scale fishing tests possible.

METHODS AND MATERIALS

Experimental Fishing

Fishing took place during five different cruises of the research vessel Charles H. Gilbert in Hawaiian waters in 1967 and 1968 (Table 1). Nehu, the regular skipjack tuna bait, were used as a control, and fishing data were collected from 37 of 101 schools of skipjack tuna encountered. On the first three cruises both threadfin shad and nehu were chummed alternately for 3- to 5-min periods on each of nine schools of skipjack tuna fished. On the latter two cruises the two bait species were alternated among 28 schools of skipjack tuna, except on three occasions when operational problems prevented alternation of bait.

Fishing was carried out in the following manner. Upon arrival on the fishing grounds, scouting commenced for bird flocks, which usually signify the presence of skipjack tuna schools. When approaching a fish school, the bait supplies were readied and the chummer, fishermen, and observers took their places. As the vessel crossed the head of the school, the chummer began broadcasting the bait until the school was brought to the stern and fishing started. If the attempt was unsuccessful, the ship would then return for another "pass" and the process was repeated. Several passes were usually made on each school until either the school was successfully fished or until it became obvious the school was not going to respond and was abandoned.

The first sign that fishing would probably be successful was a surface break or splash made by the skipjack tuna feeding on bait near the stern of the vessel. When this occurred, the vessel would slow to fishing speed (ca. 2 knots), the fishermen would enter the racks, and water sprays would be turned on and directed to the sea surface just behind the vessel. Water sprays are used by the commercial skipjack tuna fishermen in Hawaii in order to improve the catch rate (Yuen, 1969). Two scientific observers helped coordinate the experiment and recorded data. One observer, stationed on the afterdeck near the chummer, recorded the number of skipjack tuna caught and the time that each bait species was used during fishing. He was in communication by telephone with the second observer, who was stationed in an underwater observation chamber located on the

Table 1.--Dates of experimental fishing and number of skipjack tuna schools fished aboard the Charles H. Gilbert.

Cruise no.	Month	Year	No. of skipjack tuna schools fished	Method of chumming
105	Oct.	1967	1	Shad and nehu alternated at intervals of 3 to 5 min.
106	Nov.	1967	4	Do.
108	Mar.-Apr.	1968	4	Do.
109	May-Aug.	1968	22	Shad and nehu alternated among schools.
110	Aug.-Sept.	1968	6	Do.

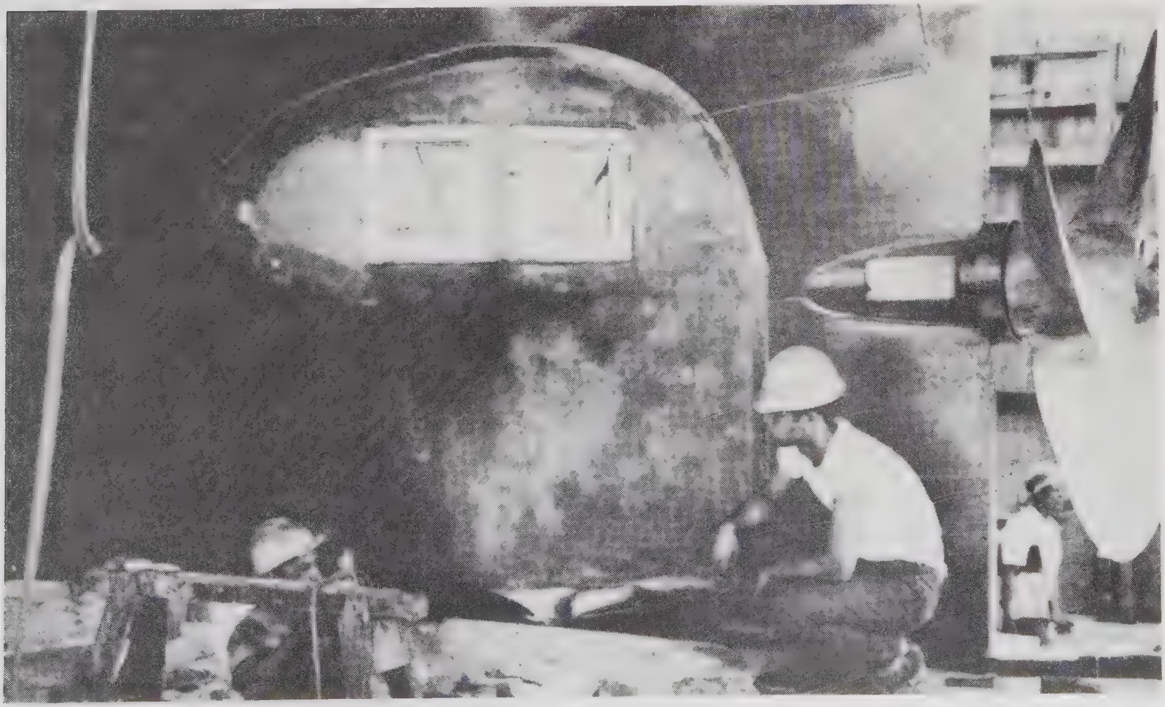

Figure 3.--Underwater observation chamber used for viewing baitfish and skipjack tuna.

portside of the ship, just forward of the propeller and below the fishing racks (Figure 3). Four experienced fishermen were in the racks during fishing and were usually the same four men during each cruise. Fishing terminated when bait was exhausted or when the school sounded, stopped biting, or bit too slowly to justify further expenditure of live bait.

Baiting

Shad captured in Wahiawa Reservoir by bait seine were transported in portable tanks by truck to Kewalo Basin, Honolulu, and acclimated to 100% seawater in 34,850-liter (9,200-gal) holding tanks before being placed in the baitwells of the Gilbert. Nehu were captured by bait seine in Pearl Harbor or Kaneohe Bay, Oahu, and placed directly into the baitwells. Nehu were "rested" overnight in the baitwells prior to departure for the fishing grounds. Shad were acclimated to seawater for 36 to 72 hr before being placed in the Gilbert's baitwells several hours prior to departure. The shad and nehu used as bait ranged from about 40 to 65 mm.

The unit of bait measure in the Hawaiian skipjack tuna fishery is the "bucket," so named because the fishermen use stainless steel buckets to transfer the bait from the bait seine to the baitwells. A bucket is equal to about 3.2 kg of baitfish. However, a bucket of nehu contains more individuals than a bucket of shad because shad are more deep-bodied than the nehu. In general, it was possible to carry a greater number of buckets of shad than nehu in the same sized baitwell because of the greater hardiness of shad.

Recording of Data

On Gilbert cruises 105 and 106 the catch data were recorded by the observer on deck using a hand tally, a stopwatch, and a wristwatch to time the start and end of fishing periods and other events. On cruises 108, 109, and 110, data collecting was automated by the use of an event recorder and a camera to automatically photograph skipjack in the fishing area through the windows of the underwater observation chamber. The catch of tuna and other information concerning fishing were graphically recorded on a 20-channel event recorder. The event recorder received data from a small hand-held control panel operated by the scientist on deck and also data from the automatically run camera in the stern observation chamber. One channel recorded the time each photograph was taken. Photographs were taken to determine if either bait resulted in a greater concentration of tuna near the hooks. A photograph was taken every 10 sec with 16-mm color film in a cinecamera operated in a single frame mode. Shutter speed was 0.03 sec. The film was analyzed by projecting the sequence, one frame at a time, and counting the number of skipjack tuna present in each frame. Only those frames taken during the time fish were actually caught were used to calculate the concentration of skipjack near the hooks.

Behavioral Observations

Observations on the swimming behavior of shad and nehu and their reaction to predation by skipjack tuna were made during fishing on Gilbert cruises 105, 106, 108, 109, and 110, and also during some preliminary trials during 1967 on Gilbert cruises 99, 100, and 102. These observations were made from the stern underwater observation chamber and also by scuba divers. The scientist in the stern chamber made continuous voice tape recordings of his visual observations of shad, nehu, and skipjack tuna. The divers observed bait behavior while swimming in the water adjacent to the stern with the ship stopped. On several occasions the divers observed shad and nehu from an underwater sea sled while it was towed from the stern of the Gilbert.

Statistical Methods

The response of skipjack tuna schools to the pole-and-line fishing method is highly variable and the frequency of various measures of response is not normally distributed (Yuen, 1959). Nonparametric statistical tests were used to analyze the data because they do not require a normal distribution. The Wilcoxon matched-pairs, signed-ranks test and the Mann-Whitney U-test (Siegel, 1956) were used.

RESULTS

Experimental Fishing

Alternating shad and nehu among schools.— Results of experimental fishing on cruises 109 and 110 are summarized in Table 2. These results are presented first because they account for 76% of the schools fished. The basic catch data for each school are given in Table 3. Inspection of Table 2 shows that shad compared favorably with nehu as a live bait, and this is confirmed

Table 2.--Summary of experimental fishing for skipjack tuna with threadfin shad and nehu alternated as bait among schools on Charles H. Gilbert cruises 109 and 110.

Item	Shad	Nehu
Number of schools chummed	28	39
Number of schools fished	14	14
Percent of schools fished	50.0	35.9
Average number of skipjack tuna caught per minute (4 men fishing)	7.5	8.2
Number of skipjack tuna caught	1,428	1,597
Average number of skipjack tuna caught per school	102	114
Total weight (kg) of skipjack tuna caught	4,809	6,788
Average total weight (kg) of skipjack tuna caught per school	344	485
Average catch per minute of skipjack tuna <4.5 kg	10.0	10.0
Average catch per minute of skipjack tuna >4.5 kg	3.0	4.9
Average duration (minutes) of fishing per school	10.8	15.4
Average number of buckets of bait used per school fished	4.0	4.8
Average weight (kg) of skipjack tuna caught per bucket of bait	85	102

Table 3.--Results of experimental fishing with threadfin shad and nehu on Charles H. Gilbert cruises 109 and 110.

Cruise no.	Station	Time fished		Total skipjack tuna catch				Average skipjack tuna weight		Amount of bait used		Average skipjack tuna catch per minute	
		Shad	Nehu	Shad	Nehu	Shad	Nehu	Shad	Nehu	Shad	Nehu	Shad	Nehu
		Minute		Number		Kg		Kg		Bucket		Number	
109	7	1.1	-	1	-	9.7	-	9.7	-	3.0	-	0.9	-
	8	-	16.0	-	58	-	323.5	-	5.6	-	3.5	-	3.6
	11	5.6	-	11	-	648.5	-	5.9	-	3.5	-	2.0	-
	14	7.4	-	53	-	326.9	-	6.2	-	3.0	-	7.1	-
	15	-	6.2	-	66	-	281.4	-	4.3	-	3.0	-	10.6
	26	3.0	-	17	-	39.3	-	2.3	-	2.5	-	5.6	-
	27	-	18.0	-	102	-	222.0	-	2.2	-	3.0	-	5.7
	28	18.0	-	153	-	388.6	-	2.5	-	7.0	-	8.5	-
	29	-	5.2	-	33	-	320.3	-	9.7	-	4.0	-	6.3
	31	12.4	-	84	-	129.5	-	1.5	-	3.5	-	6.8	-
	32	-	11.5	-	217	-	334.6	-	1.5	-	5.0	-	18.9
	35	1.5	-	1	-	5.1	-	5.1	-	2.0	-	0.6	-
	36	-	12.4	-	105	-	390.5	-	3.7	-	3.5	-	8.5
	42	11.0	-	93	-	215.1	-	2.3	-	2.5	-	8.5	-
	43	-	20.7	-	312	-	622.6	-	2.0	-	10.0	-	15.1
	44	7.9	-	32	-	68.2	-	2.1	-	2.0	-	4.1	-
	46	-	5.5	-	67	-	118.5	-	1.8	-	2.5	-	12.2
	47	1.5	-	20	-	30.8	-	1.5	-	2.0	-	13.6	-
	48	23.6	-	464	-	799.6	-	1.7	-	7.0	-	19.7	-
	52	-	20.8	-	184	-	1,368.5	-	7.4	-	8.5	-	8.9
	53	16.8	-	312	-	905.6	-	2.9	-	6.5	-	18.6	-
	70	-	13.4	-	106	-	182.7	-	1.7	-	3.0	-	7.9
110	6	-	38.2	-	165	-	1,878.2	-	11.4	-	9.0	-	4.3
	7	25.6	-	114	-	1,096.0	-	9.6	-	10.0	-	4.4	-
	12	-	17.3	-	70	-	241.3	-	3.4	-	5.0	-	4.0
	13	16.3	-	73	-	145.7	-	2.0	-	2.0	-	4.5	-
	14	-	18.4	-	29	-	218.3	-	7.5	-	2.5	-	1.6
	31	-	12.4	-	83	-	286.1	-	3.4	-	4.0	-	6.7
	Totals	151.7	216.0	1,428	1,597	4,808.6	6,788.5	4.0	4.7	4.0	4.8	7.5	8.2

by the results of the statistical analyses (see Table 4). All tests indicated no significant differences between shad and nehu at the 0.05 probability level.

Alternation of both shad and nehu on the same school.— Results of experimental fishing during cruises 105, 106, and 108 are summarized in Table 5. The basic catch data for these three cruises are given in Table 6. These results also show shad compared favorably with nehu as live bait. Analysis of the skipjack tuna catch per minute showed no significant difference between either shad or nehu as bait (see Table 4). Additional statistical tests were not made because further stratification of the data would have considerably reduced the sample size. Information on the amount of shad and nehu chummed at each station was not collected because this would have required temporarily suspending chumming at the end of each period with the result that the school of skipjack tuna probably would have sounded and fishing ended.

Number of skipjack tuna in the fishing area.— Estimates of the concentration of skipjack tuna in the fishing area near the hooks are given in Table 7. Mean values for cruises 108, 109, and 110 ranged from 1.7 skipjack tuna per photograph with nehu during cruise 108 to 5.0

Table 4.--Summary of analyses made to compare the effectiveness of threadfin shad with nehu as a live bait during Charles H. Gilbert cruises 105, 106, 108, 109, and 110. All tests indicated no significant differences between shad and nehu at the 0.05 probability level.

Cruise no.	Statistic compared, shad versus nehu	Analysis used	N	Value calculated	Probability of occurrence
109, 110	Skipjack tuna catch per minute	Mann-Whitney U-test	28	U = 86	>0.10
	Skipjack tuna <4.5 kg, catch per minute	do.	18	U = 39	>0.10
	Skipjack tuna >4.5 kg, catch per minute	do.	10	U = 8	≥0.42
	Number of skipjack tuna caught per school	do.	28	U = 70.5	>0.10
	Duration of fishing per school	do.	28	U = 68	>0.10
	Total weight of skipjack tuna caught per school	do.	28	U = 59	>0.05
105, 106, 108	Skipjack tuna catch per minute	Wilcoxon matched-pairs, signed-ranks test	18	T = 16	>0.05

Table 5.--Summary of experimental fishing for skipjack tuna with both threadfin shad and nehu alternated as bait on the same school during Charles H. Gilbert cruises 105, 106, and 108.

Item	Shad	Nehu
Number of schools first chummed with	25	9
Number of schools responding to first bait chummed	3	[1]5
Percent of schools responding to first bait chummed	12.0	55.6
Number of schools fished with both baits	9	9
Total number of fishing periods for each bait	37	38
Average number of skipjack tuna caught per minute (4 men fishing)	9.1	7.7
Number of skipjack tuna caught	1,248	998
Total weight (kg) of skipjack tuna caught	4,147	2,823
Average number of skipjack tuna caught per school	139	111
Average total weight (kg) of skipjack tuna caught per school	461	314
Average catch per minute of skipjack tuna <4.5 kg	10.0	9.0
Average catch per minute of skipjack tuna >4.5 kg	7.3	5.7

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[1] One school was first chummed with shad, but did not respond until nehu was chummed.

Table 6.--Results of experimental fishing with threadfin shad and nehu on _Charles H. Gilbert_ cruises 105, 106, and 108.

Cruise no.	Station	Fishing periods		Time fished		Total skipjack tuna catch				Average skipjack tuna weight	Average skipjack tuna catch per minute	
		Shad	Nehu	Shad	Nehu	Shad	Nehu	Shad	Nehu		Shad	Nehu
		Number		Minute		Number		Kg		Kg	Number	
105	4	2	3	6.0	9.0	42	55	91.4	119.7	2.2	7.0	6.1
106	5	4	3	18.5	14.5	128	90	725.6	510.2	5.7	6.9	6.2
	6	3	3	9.0	8.5	143	65	531.8	241.7	3.7	15.9	7.6
	8	5	5	15.5	14.5	158	32	895.7	181.4	5.7	10.2	2.2
	9	1	1	9.0	3.0	42	26	259.0	160.4	6.2	4.7	8.7
108	11	6	6	17.8	18.2	191	168	389.8	342.9	2.0	10.7	9.2
	12	9	9	26.8	26.3	435	383	986.4	868.5	2.3	16.2	14.6
	15	3	4	8.8	12.0	31	82	38.0	112.7	1.2	3.5	6.8
	20	4	4	11.0	12.1	78	97	229.0	285.9	2.9	7.1	8.0
	Totals	37	38	122.4	118.1	1,248	998	4,146.7	2,823.4	3.5	9.1	7.7

Table 7.--Number of skipjack tuna photographed in the fishing area.

Cruise no.	Bait	No. of schools	No. of photos	No. of skipjack tuna	Average no. of skipjack tuna per photograph
108	Shad	4	389	1,159	3.0
	Nehu	4	419	730	1.7
109	Shad	11	588	2,777	4.7
	Nehu	8	517	2,149	4.2
110	Shad	2	233	839	3.6
	Nehu	4	535	2,677	5.0
Totals	Shad	17	1,210	4,775	3.8
	Nehu	16	1,471	5,556	3.6

skipjack tuna per photograph with nehu during cruise 110. The mean value for all three cruises was 3.8 skipjack tuna per photograph with shad and 3.6 skipjack tuna per photograph with nehu.

The number of skipjack tuna counted per photograph should be considered only as rough indications of the concentration of skipjack in the fishing area because of certain inherent variables associated with the photography. These included the rolling motion of the vessel, skipjack tuna being obscured by bubbles, changes in lighting conditions caused by clouds and vessel maneuvers, and the relatively slow camera shutter speed.

Behavior of Bait

Generally speaking, threadfin shad and nehu had similar swimming behavior when used as chum for skipjack tuna fishing. Some differences occurred in their behavior, however, and were marked enough to allow an experienced observer to usually determine which species was being chummed.

Upon entering the water, both species dove downward to escape the skipjack. The diving angle of nehu varied up to 90°, but typically was 45° to 90°. They appeared to dive faster than shad and exhibited marked dodging in their escape attempts. If several nehu landed in the water in the same vicinity, they often formed a school a few feet below the surface and tried to dive downward and escape en masse. The diving angle of shad also varied up to 90°, but was usually about 45° to 65°, generally not as steep as that of nehu. They did not appear to swim as fast as nehu, nor dodge quite as vigorously. Shad also formed small schools while diving. During fishing, shad were often eaten by the skipjack tuna before they had a chance to get much deeper than 3 to 4 m, while nehu often reached depths of 6 to 8 m before being eaten. This sometimes resulted in the skipjack tuna swimming deeper when nehu was being chummed than on those schools when the bait species were alternated.

Both baits, however, can dive to considerable depths. From a sea sled we have observed nehu swim as deep as 18 m. They were still heading downward when lost to view. On one occasion scuba divers followed two shad and one Tilapia mossambica down to 23 m before breaking off the pursuit.

One difference between the two baits is their visibility. Shad are deeper bodied than nehu and have a greater portion of their sides covered with silvery scales. The result is a larger silvery reflecting surface. To the underwater observer, shad is more visible than nehu. Shad scales are highly deciduous and create a pattern of small silvery points of reflected light in the water. On one occasion, observers on the sea sled 23 m astern of the Gilbert were able to determine when a switch in bait from nehu to shad occurred just by watching for the silvery glints in the water from the shad scales.

Both shad and nehu have been observed to return to the surface when pursued by skipjack and to flee to the side of the vessel and swim along beside it. Whether this occurs more frequently when using shad or nehu is not known. Both shad and nehu are avidly eaten by skipjack; we have found skipjack stomachs gorged with shad, nehu, and both.

DISCUSSION

Bait Characteristics

The basic characteristics necessary for a live bait to be effective in the Hawaiian skipjack tuna fishery are the ability to: (1) lure skipjack to the stern of the fishing vessel, (2) concentrate the skipjack at the stern in sufficient numbers, and (3) produce a good catch rate. If the bait can be easily obtained, is hardy, and is readily handled, its effectiveness should increase.

Threadfin shad satisfy the three basic characteristics, and are also hardy and readily handled. During Gilbert cruises 109 and 110, shad were more successful than nehu in luring skipjack tuna to the stern of the vessel, since 50.0% of the schools chummed with shad were successfully fished and 35.9% of the schools chummed with nehu were fished. On cruises 105, 106, and 108, nehu were more successful than shad; 55.6% of the schools initially chummed with nehu were successfully fished and 12.0% of the schools initially chummed with shad were successfully fished. With the exception of shad on cruises 105, 106, and 108, these percentages are roughly comparable to those reported by Royce and Otsu (1955), who found that only 43% of Hawaii skipjack tuna schools are successfully fished, and Yuen (1959), who reported a 48% response to nehu. The low percentage response to shad on cruises 105, 106, and 108 was due to the necessity of initially chumming shad on successive schools in order to conserve low supplies of nehu. Had nehu been chummed on alternate schools, the percent response for both baits probably would have been similar.

The ability of shad to produce catches comparable to nehu is shown in the summaries given in Tables 2 and 5. On cruises 109 and 110, shad produced a catch rate of 7.5 skipjack tuna per minute, slightly less than the nehu catch rate of 8.2 skipjack tuna per minute. On cruises 105, 106, and 108, the catch rate averaged 9.1 skipjack tuna per minute with shad, slightly better than that of 7.7 skipjack tuna per minute with nehu.

The major differences between shad and nehu during cruises 109 and 110 were in the total weight of skipjack tuna caught and in the duration of fishing. The higher weight of skipjack tuna caught with nehu on cruises 109 and 110 was due to large skipjack tuna being heavily fished from several schools when nehu were used as bait, such as station 52, cruise 109, and station 6, cruise 110. Since the bait species were switched on each school, and there is no prior way of knowing what size skipjack tuna are in successive schools, it appears the difference is due to chance. The lower duration of fishing with shad (10.8 min) is due to the effects of two schools (cruise 109, stations 7 and 35) when only one skipjack tuna was caught from each. If data from these two schools are removed, the mean duration of fishing with shad for both cruises becomes 12.4 min, compared with nehu at 15.4 min.

The amount of bait necessary to produce a good skipjack tuna catch is another important factor in developing an alternate live bait. Here shad also appear promising. During cruises 109 and 110, an average of 4.0 buckets of shad and 4.8 buckets of nehu were used on each school successfully fished. These amounts were calculated from the chummer's estimate of how much bait had been used, the estimate being made just after fishing ended.

In considering bait requirements, the effects of mortality must also be taken into account. Brock and Uchida (1968) found that nehu usually averaged about 25% mortality a day after being placed in the baitwells. I have no exactly comparable data for shad, since the shad were not placed directly into the baitwells but were placed first into 2,350-liter (620-gal) portable transfer tanks and then into the larger 34,850-liter (9,200-gal) holding tanks for several days prior to being placed into the baitwells. However, it was nct unusual to place about 10,000 to 15,000 shad in a 2,350-liter oxygenated tank, transport them for 37 km from the reservoir to the larger holding tanks and find less than 50 dead shad on arrival. In placing shad aboard several vessels using a variety of transfer methods on other occasions, the average mortality the following day was 16% (Iversen and Puffinburger[1]). Assuming optimum transfer conditions, a mortality rate of 10% by the following day appears attainable. During Gilbert cruise 116, 113 buckets of shad were carried in the ship's baitwells and 30 buckets in portable tanks on deck a distance of 4,300 km southeast of Hawaii for use as live bait in skipjack tuna fishing (Hida, 1970). Although mortalities in the portable tanks were about 50% due to bait being lost through open seams in the tank covers, mortalities in the regular baitwells were negligible.

Use of a live bait with a lower mortality rate than nehu could result in a reduced overall bait requirement, but only if the fishing effort remained unchanged. A reduced bait requirement is unlikely to happen because the purpose of developing a substitute bait is to increase fishing effort. What is more likely to happen is that use of a hardy bait will allow fishermen to increase the number of trips, fish farther offshore, or possibly increase the duration of each fishing trip. Presently most trips last 1 day and the boats rarely fish more than 170 km from the islands (Uchida, 1967). The net result could well be an increase in the total amount of bait needed.

The availability of bait-sized shad must also be considered. Landings of skipjack tuna in Hawaii are highest during the months of June through August, lowest in November through March, and intermediate in the remaining months (Brock and Uchida, 1968). In Hawaii shad begin to spawn in the late winter and early spring, with the heaviest spawning apparently occurring in February and March. In about 10 to 12 weeks the young shad grow to 40 to 50 mm and are large enough to use as bait. The availability of bait-sized shad thus coincides with the heaviest demands for bait from the fishermen during the summer. Bait-sized shad must also be abundant enough to meet needs. In recent years, the annual catch of nehu has averaged about 24,500 buckets (Uchida, 1967). It is not known how large an impoundment would be required to produce that many buckets of shad. During 16 days of baiting in Wahiawa Reservoir between February 18 and June 15, 1970, we captured 1,025 buckets of shad, an average of 64 buckets per day. More could have been captured, for the amount removed was limited by the carrying capacity of our portable tanks. Wahiawa Reservoir probably contains at least 5,000 buckets of shad in the summer. The reservoir has a surface area of 122 ha (302 acres) at high water. Thus it may be possible to culture enough shad in a pond or impoundment approaching the size of Wahiawa Reservoir to satisfy a significant percentage of the fleet's total bait requirements, providing the cost of culturing, capturing, and acclimatizing the shad is economically feasible.

What Remains to be Done?

On a short-term basis, the next logical step is a comprehensive sea test under actual commercial conditions. Providing enough shad to one or more commercial boats so that they could fish exclusively with shad during all or part of the peak fishing months would produce information on fishing effort and catches due to the use of a substitute live bait. More precise information is also needed on the amount of shad that can be cultured in ponds of different sizes and on the costs of shad culture. The results of a comprehensive commercial fishing test and cost estimates for culturing shad should lead to a rational decision on the economic feasibility of using shad as a substitute live bait for nehu.

On a long-term basis, biological investigations are needed to determine if the shad's reproductive cycle can be manipulated to produce earlier spawning and if it is possible to raise shad on a large scale in a bait hatchery.

SUMMARY

1. In order to compare the effectiveness of threadfin shad with the anchovy (nehu) normally used as live bait for skipjack tuna fishing in Hawaii, 37 schools of skipjack tuna were fished

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[1] Iversen, Robert T. B., and Jay O. Puffinburger. Capture, transportation, and pumping of threadfin shad, Dorosoma petenense. Unpublished MS.

with the two baits during 1967 and 1968 aboard the research vessel Charles H. Gilbert. Threadfin shad and nehu were alternated among 25 of 28 skipjack schools fished and alternated every 3 to 5 min on each of the other 9 skipjack schools.

2. When bait was alternated among schools, the following catch data were recorded. Average number of skipjack tuna caught per minute: shad - 7.5; nehu - 8.2. Number of skipjack tuna caught: shad - 1,428; nehu - 1,597. Average number of skipjack tuna caught per school: shad - 102; nehu - 114. Average weight of skipjack tuna caught per school: shad - 344 kg; nehu - 485 kg. Average duration of fishing per school: shad - 10.8 min; nehu - 15.4 min. Percent of schools chummed that were successfully fished: shad - 50.0; nehu - 35.9.

3. When bait was alternated on the same school, the following catch data were recorded. Average number of skipjack tuna caught per minute: shad - 9.1; nehu - 7.7. Number of skipjack tuna caught: shad - 1,248; nehu - 998. Average number of skipjack tuna caught per school: shad - 139; nehu - 111. Average weight of skipjack tuna caught per school: shad - 461 kg; nehu - 314 kg. Percent of schools responding to first bait chummed: shad - 12.0; nehu - 55.6.

4. Nonparametric statistical tests showed no significant differences between threadfin shad and nehu in the following categories of catch data: skipjack tuna catch per minute, catch per minute of skipjack tuna < 4.5 kg, catch per minute of skipjack tuna >4.5 kg, number of skipjack tuna caught per school, duration of fishing per school, and weight of skipjack tuna caught per school.

5. Underwater photographs taken automatically indicated shad concentrated skipjack tuna in the fishing area equally as well as nehu.

6. Threadfin shad and nehu have similar swimming behavior when used as chum for skipjack tuna fishing.

7. Bait-sized threadfin shad occur in Hawaiian freshwater impoundments during the peak months of skipjack tuna fishing. They are hardy, readily handled in large numbers and easily acclimated to salt water.

ACKNOWLEDGMENTS

I would like to acknowledge the capable assistance of the captain and crew of the Charles H. Gilbert, without whose help the shad could not have been captured or tested at sea, and of my colleagues Reginald M. Gooding, Eugene L. Nakamura, Earl Murchison, John J. Naughton, and Randolph K. C. Chang, for their unstinting cooperation in conducting the experiments and making bait observations at sea. I thank Richard N. Uchida and Eugene L. Nakamura for reviewing the manuscript.

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Isistius brasiliensis, A SQUALOID SHARK, THE PROBABLE CAUSE OF CRATER WOUNDS ON FISHES AND CETACEANS

EVERET C. JONES[1]

ABSTRACT

Evidence is presented that bites inflicted by the small squaloid shark, *Isistius brasiliensis* (Quoy and Gaimard), are the causes of crater wounds, crescentic wounds, and related scars on large pelagic fishes and cetaceans. This evidence consists of a crescentic "wound" experimentally produced on the side of a dead fish by a living *Isistius*; specialized morphology of the shark's basihyoid cartilage and coracohyoideus muscles, lips, labial cartilages, and spiracles, that, together, enable the shark to form an oral vacuum on a smooth surface; an experiment in which a living *Isistius* formed such a vacuum; specialized morphology and arrangement of the mandibular teeth; close agreement between the range of reported wound widths and the estimated range of bite widths of *Isistius;* agreement between the geographical ranges of *Isistius* and those fishes and cetaceans which bear crater wounds; and, finally, the presence in *Isistius* stomachs of hemispheroidal plugs of fish flesh. Speculation on the circumstances that may enable a small, slow shark to make contact with large, swift fishes and cetaceans is included. *Isistius* apparently qualifies as a temporary parasite.

Probably the earliest account of the existence of small, round or oval, scooped-out wounds on the sides of large pelagic fishes is contained in an ancient legend of Samoa (A. Utu, personal communication), which states that atu (skipjack tuna, *Euthynnus pelamis* (Linnaeus)) entered Palauli Bay, and, upon approaching the beach, left small round pieces of their flesh as gifts to Tautunu, chief of that community. Evidence of this sacrifice was found by the people who caught the atu and observed fresh, round wounds on their sides.

This legend provides one of many explanations that have been advanced regarding the causes of such wounds on large pelagic fishes as well as on whales and porpoises. This paper presents evidence that many crater wounds, crescentic wounds, and the resulting scars on pelagic fishes (Figure 1), and open pit wounds and resulting scars on cetaceans are the results of bites inflicted by the small squaloid shark, *Isistius brasiliensis* (Quoy and Gaimard). (A second species, *Isistius plutodus,* was described by Garrick and Springer (1964) from the Gulf of Mexico. Although nothing is known of the behavior of this species, which is based on one specimen, it is probable that its feeding habits are similar to those of *I. brasiliensis.*)

Such wounds on fishes have been reported by Nemoto (1955), Iversen (1959), Guitart M. (1964), Klawe (1966), Bane (1969), and Machado Cruz (1969). The literature on open pit wounds and related scars on cetaceans is much more extensive, apparently beginning with the work of Collett (1886). Mackintosh and Wheeler (1929) and van Utrecht (1959) presented thorough discussions of these wounds and probable causes, and summarized the previous literature. Nemoto (1955) noted that some of the wounds observed on whales are similar to and probably have a common origin with those on fishes. He further stated that a cause other than lamprey attacks, the most commonly advocated agent, must be found to account for crescent-shaped scars and open pit wounds on cetaceans and fishes.

It was not always possible for me to determine whether published photographs and descriptions were of wounds and scars of the types which I attribute to *Isistius* bites. I have never seen wounds known to have been produced by lampreys and therefore cannot comment with any

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[1] National Marine Fisheries Service, Hawaii Area Fishery Research Center, Honolulu, Hawaii 96812.

Manuscript accepted June 1971.

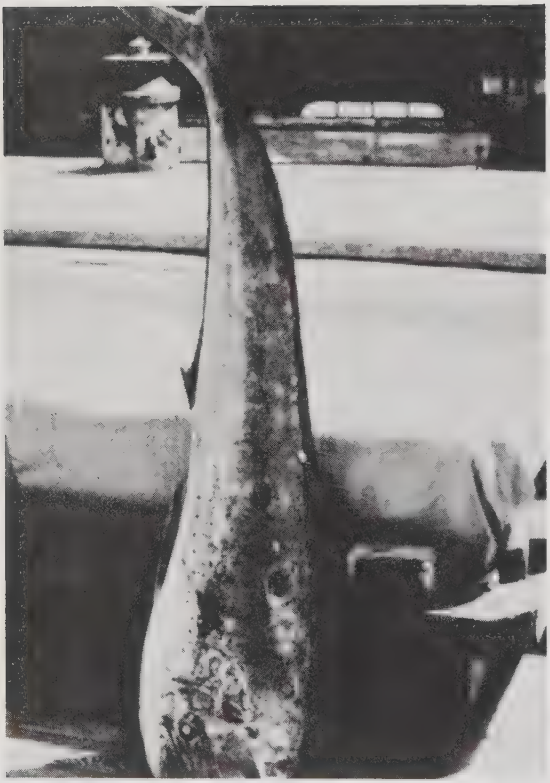

FIGURE 1.—Crater wounds on a large dolphin from the central Pacific.

authority on them. I believe, however, that Pike (1951) unknowingly but accurately described the differences between lamprey bites and *Isistius* bites on whales when he wrote: "The lampreys seem to leave two distinct types of wounds . . . . The first consists of a circular area in which the epidermis is completely abraded by the teeth of the sucking disc. In the center of this is a hole through the skin caused by the rasping tongue. In the other type the lamprey apparently rasps away the skin over the entire area with the result that there is a circular sore right down to the blubber and no periphery of skin which has been damaged but not eaten away." The second type and some of the wounds and scars illustrated by Pike are, I believe, attributable to *Isistius* bites.

Crater wounds have been reported in the literature cited on skipjack tuna; yellowfin tuna, *Thunnus albacares* (Bonnaterre); dolphin, *Coryphaena hippurus* Linnaeus; opah, *Lampris regius* (Bonnaterre); and swordfish, *Xiphias gladius* (Linnaeus) (Figure 2). In addition to these, I have seen crater wounds on albacore, *Thunnus alalunga* (Bonnaterre), and wahoo, *Acanthocybium solandri* (Cuvier), in the central Pacific. Biologists and fishermen in Hawaii have reported to me having seen them on kawakawa, *Euthynnus affinis* (Cantor); large jacks, *Caranx* sp.; rainbow runners, *Elagatis* sp.; and various species of marlins, *Istiophoridae*.

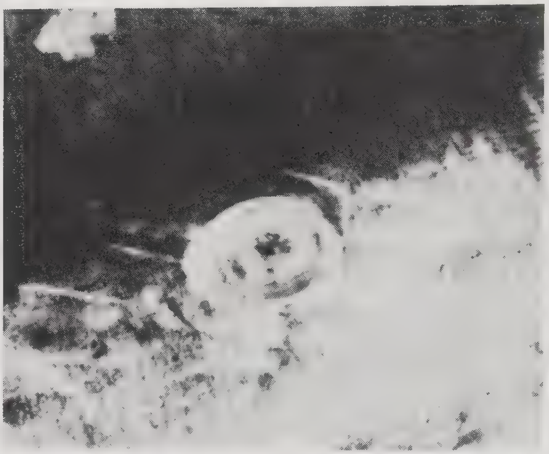

FIGURE 2.—A crater wound on the side of a swordfish caught in the Gulf of Mexico. (Photo by Martin Bartlett.)

The cetaceans upon which crater wounds, crescentic wounds, or resultant scars have been reported were listed by van Utrecht (1959). Included were beaked whales, sperm whales, various species of porpoises, and nearly all of the baleen whales (order Mysticeti) except the right whales (family Balenidae) which apparently do not migrate out of cold polar waters. In Hawaiian waters, wounds and scars (Figure 3) are commonly seen on porpoises of the genera *Tursiops* and *Stenella*, and have been observed on a beaked whale, *Ziphias* sp., stranded on Oahu.

Dr. Donald W. Strasburg, during discussions several years ago, planted the idea that *Isistius* might be the cause of crater wounds on fishes. He had found (Strasburg, 1963) that the man-

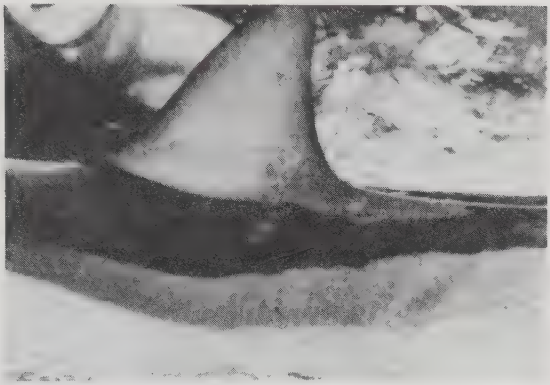

FIGURE 3.—Crescentic scar on a living porpoise, *Stenella roseiventris* Wagner, The Oceanic Institute, Makapuu, Hawaii.

dibular teeth of *Isistius* are shed as a unit and that the next set of replacement teeth are already erect and immediately functional when the previous set is shed. He wondered " . . . which aspects of *Isistius* biology require such a safeguard."

OBSERVATIONS

An opportunity to test the idea came in July 1969, during cruise 44 of the RV *Townsend Cromwell* of the NMFS, HAFRC (National Marine Fisheries Service, Hawaii Area Fishery Research Center). Nightly midwater trawl hauls were made along long 145° W between lat 14° N and 3° S in the central Pacific. The trawl catches contained occasional specimens of *Isistius*, some of which were alive but moribund when brought on board. I stated that this species of shark might be responsible for the crater wounds which we had observed on tunas a few hours earlier. This led John D. Fowler, Jr., research assistant aboard the *Townsend Cromwell*, to press the mouth of a moribund *Isistius* against the side of a dead fish, *Cubiceps* sp. The shark made a biting motion, producing a crescentic wound (Figure 4) that if completed would have been similar in size and shape to crater wounds observed on tunas. That shark could not be induced to repeat its performance, but Fowler's experiment led to further attempts to determine whether adaptations in structure for specialized feeding behavior existed in *Isistius*.

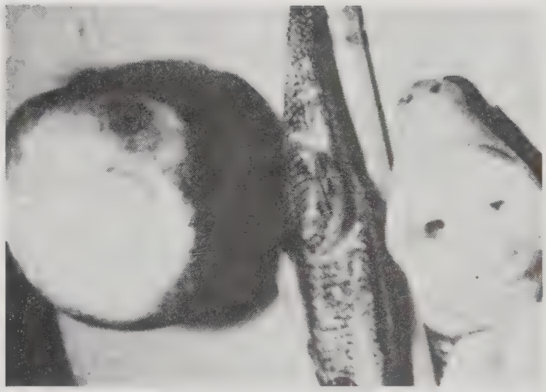

FIGURE 4.—A crater "wound" produced on the surface of a nectarine by pushing the teeth of a dead *Isistius* into the fruit and then rotating the body of the shark around the point of attachment. In the center is a crescentic "wound" produced by a living *Isistius* when its mouth was pressed against the side of the dead fish.

The basihyoid cartilage or "tongue" of *Isistius* was large and thick in contrast to that structure in galeoid sharks. It was also unusually movable; with a pencil I was able to push the tongue caudad to a point just anterior to the first exterior gill opening (Figure 5). In that position the posterior margin of the tongue was elevated (dorsad) until the tongue was nearly vertical, fitting closely against the roof of the mouth, and

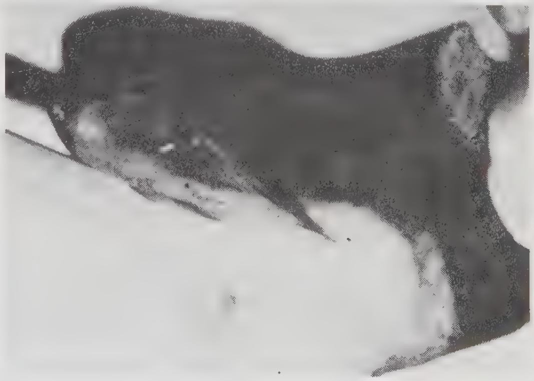

FIGURE 5.—A demonstration of the movability of the tongue of *Isistius*.

completely separating the mouth from the pharynx. Two ridges in the roof of the mouth corresponded to two grooves in the posterior margin of the tongue. This structural correspondence suggested that vertical positioning of the tongue was a normal occurrence. The movability of the tongue, as well as several other attributes described below, can only be demonstrated with specimens of *Isistius* that have not been fixed.

Observations of these anatomical characters led to the hypothesis that *Isistius* is capable of achieving a vacuum with its mouth on a smooth surface. Concurrently with the retracted, vertical positioning of the tongue, the lips protruded completely around the mouth. The fleshy lateral lips contained well-developed labial cartilages that caused them to be semirigid and, when protruded, to complete an ovoid of labial margins in a single plane (Figure 6). Such a structure in contact with a smooth surface enables the shark to form a vacuum when the spiracles are closed and the tongue then retracted.

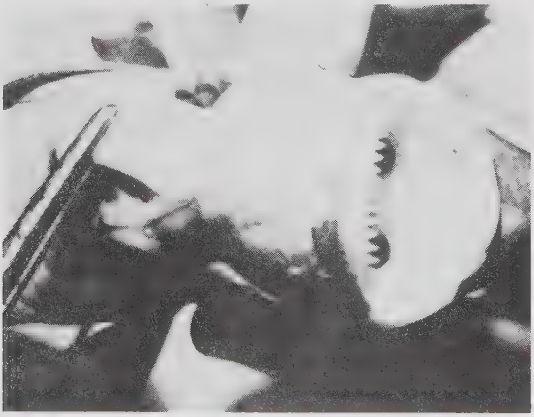

FIGURE 6.—A demonstration of the coracohyoideus muscles of *Isistius*. Note also the protruded lips, the internal openings of the spiracles, and the mandibular teeth.

In order to further determine if behavioral retraction of the tongue was probable, dissections were made of the ventral surface of the shark just posterior to the mandible. The paired coracohyoideus muscles that insert on the tongue were unusually large in *Isistius* (Figure 6). A comparative dissection of a large, fresh, whitetip shark, *Carcharhinus longimanus* (Poey) was made (Figure 7); the cross sectional areas in *Isistius* were estimated to be four times those of the same muscles in the whitetip shark, both relative to the total lengths of the sharks. Pulling caudad on the exposed coracohyoideus muscles of *Isistius* caused the tongue to retract to the nearly vertical position noted before; concurrently, the mouth gaped and the lips protruded. The tongue of the whitetip shark was not movable and pulling on the coracohyoideus muscles did not retract it.

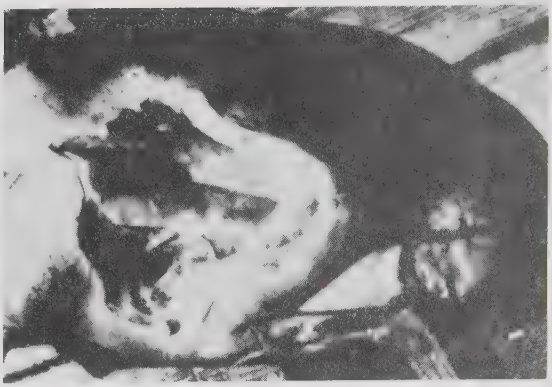

FIGURE 7.—Exposed coracohyoideus muscles of a large whitetip shark, central Pacific.

Later I attempted to repeat Fowler's experiment by holding the mouth of a living *Isistius* against the side of a gempylid fish. In this case, the shark did not make a biting motion but, instead, the spiracles closed, the head flattened slightly, and an oral vacuum was formed by means of which I was able to lift the gempylid from the table with no other support.

It seemed that the remaining evidence needed to indict *Isistius* would be the presence of hemispheroidal plugs of fish flesh in their stomach contents. This evidence was found when two *Isistius* caught subsequently on the same cruise were found to contain single plugs of flesh of appropriate size and shape. One of these plugs was from a relatively large fish, judging from the thickness of the myomeres; the other was from a squid. During a later cruise in the same area, Reginald M. Gooding, fishery biologist,

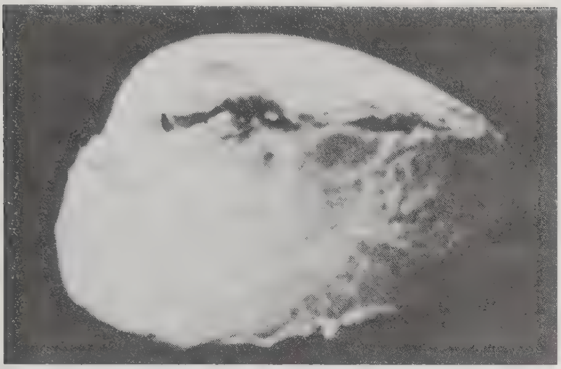

FIGURE 8.—A hemispheroidal plug of unidentified fish flesh from the stomach of an *Isistius*, central Pacific.

found a very fresh plug of fish flesh complete with integument and some scales (Figure 8). The fishes from which these plugs were bitten have not been identified. In order to find such plugs, it is necessary to examine *Isistius* immediately after capture because digestion will usually continue for a time after the specimen is placed in formaldehyde or a freezer.

DISCUSSION

Further evidence relating *Isistius* to wounds on fishes may be present in a photograph (Figure 9) of a crescentic wound on the caudal fin of a swordfish (M. R. Bartlett, personal communication). The deep crescentic cut is opposed by an arc of small dents and scars. The size and arrangement of these correspond to the small, hooked upper teeth of *Isistius* (Figure 6). In addition, a series of white scratches extending from the small arc toward the crescentic cut appear to have been made by the upper teeth as the shark backed away from the incomplete bite. In this case, the shark's mandibular teeth must have encountered the large, bony ray in the edge of the caudal fin. The same fin bore an entire, cut-out wound near the posterior border (Figure 10).

The geographical distribution of records of *Isistius brasiliensis* (Strasburg, 1963; Parin, 1964) corresponds well with the general distributions of the species of fishes which bear crater wounds. Several authors (Mackintosh and Wheeler, 1929; Pike, 1951; Nemoto, 1955; van Utrecht, 1959) have noted that fresh wounds were seen only, or more frequently, on cetaceans caught in the warmer waters of their migrations and that those caught more poleward bore only healed or partially healed scars. This was evidence, they stated, that the animal producing the wounds was an inhabitant of warm water.

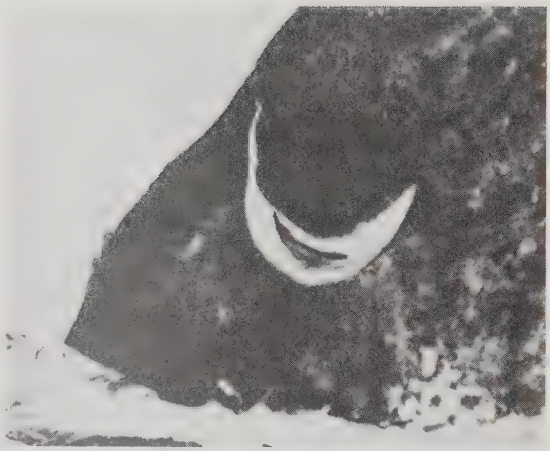

FIGURE 9.—A crescentic wound on the caudal fin of a swordfish caught in the Gulf of Mexico. Note the arc of small dents opposite the cut, and the scratches produced by the shark's upper teeth as it backed away from the incomplete wound. (Photo by Martin Bartlett.)

Some wounds on cetaceans described in the literature were undoubtedly produced by lampreys (Pike, 1951). The majority of catch records of lampreys in both the Pacific and Atlantic, however, are near shore and in temperate or cold waters which fits poorly the distribution of fishes and whales bearing fresh crater wounds.

The largest crater wounds recorded (Mackintosh and Wheeler, 1929) were 4 or 5 cm by 7 cm. The smallest I have seen were 1.2 cm by 2 cm. The smaller diameters of these correspond well with the bite-widths I have estimated for *Isistius* at the extremes of the known range of 14 to 50 cm, total lengths (Strasburg, 1963).

All of the *Isistius* stomachs examined aboard the *Townsend Cromwell* contained squid beaks and pieces of squid pens. Strasburg (1963) also

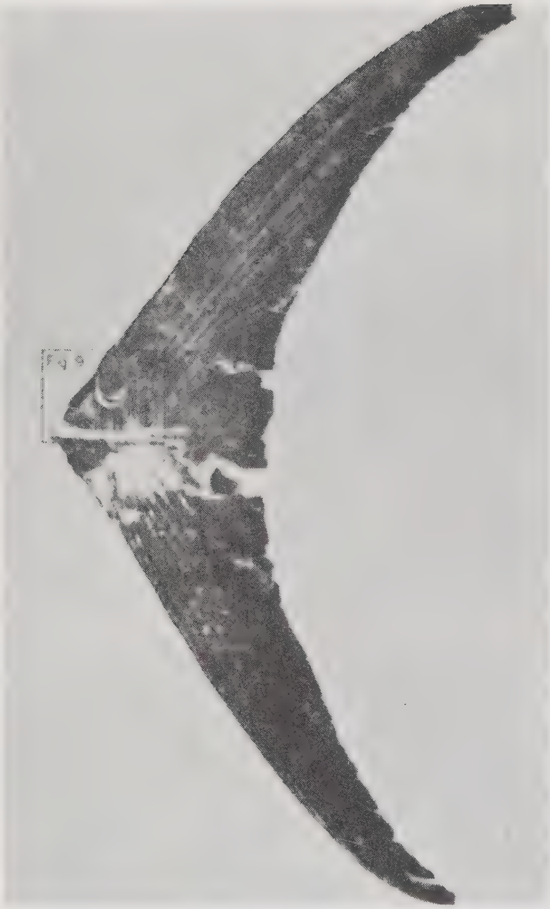

FIGURE 10.—The caudal fin of a swordfish caught in the Gulf of Mexico, showing a crescentic wound and a completed wound cut through the trailing edge of the fin.

found squid remains in most of the stomachs of preserved specimens he inspected, and calculated that the squids which were eaten were as large or larger than the sharks. He wondered how small sharks that apparently swim slowly could catch and capture such large, swift prey.

This question is also pertinent in considering how *Isistius* succeeds in contacting fast-swimming animals such as tunas, marlins, or porpoises. It would appear to be no problem for *Isistius* to approach and make contact with basking or drifting whales or fishes. In the case of tunas, however, there is no evidence that they ever drift or stop swimming (Magnuson, 1970). A possible sequence is that the potential prey, seeing *Isistius* as an object apparently suitable for food, makes the initial approach, identifies it at a short distance, rejects it as food, and veers off. At that instant, the shark may be able to achieve contact by means of a short dash.

It is also possible that the shark, to some degree, simulates other organisms such as squids in the pattern of its luminous ventral surface. A more remote possibility is that *Isistius* is mistaken by large teleosts for a cleaner, and is invited to make contact.

Large squids appear to be killed by *Isistius* more often than merely deprived of plugs of flesh. It may be that squids also make an initial approach but, unlike teleosts, do not veer off from their attack and are subsequently bested in the encounter.

Isouchi (1970) provided the only record of an *Isistius* eaten by a large teleost when he found a living shark in the stomach of *Scomberomorus* sp. This record indicates that *Isistius* is a potential food item; on the other hand, records of teleosts having ingested any species of small or young sharks are limited to five or six (S. Springer and M. R. Bartlett, personal communications). This certainly supports a hypothesis of usual rejection. Rejection of the young as food by teleosts, in fact, may account for the survival of most elasmobranch species, considering their extremely low reproduction rates and relatively low swimming speeds.

It may not be necessary to assume any complicated behavior patterns of *Isistius* or its prey; perhaps contacts by means of short dashes can be made during chance proximities. Thomas Dohl, The Oceanic Institute, Hawaii, has informed me that young porpoises of sizes that are assumed to be still nursing do not bear wounds or scars, but those which are larger do. Similar restriction of wounds and scars to older porpoises is suggested by the data of van Utrecht (1959). This may be simply a matter of an increased probability of encounter with time; but it may, on the other hand, indicate that porpoises are not attacked by *Isistius* until the porpoises become predatory on fish.

Several crescentic wounds which I have examined on tunas were made from a frontal attack

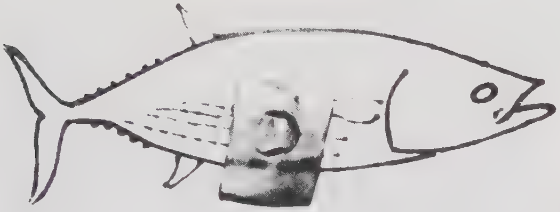

FIGURE 11.—An excised crescentic wound superimposed over a diagram of a skipjack tuna to indicate that the wound was made from a frontal attack, central Pacific.

position, that is, the shark and its prey were going in opposite directions when the wound was inflicted (Figure 11). Such crescentic wounds, as previously pointed out, are apparently the result of circumstances which do not allow the shark to complete the scooping out process. Besides providing support for the suggestion that the teleost makes the initial approach, the evidence of frontal attacks may explain the occurrence of wounds in which the plug of flesh is still attached to the bottom of the wound by a peduncle. Such wounds are common on cetaceans (Mackintosh and Wheeler, 1929; van Utrecht, 1959). In a frontal attack, the drag of water on the shark's body would cause it to rotate, in the manner of the hand of a clock, around the point of attachment until the shark was oriented in the same direction as its prey. This movement would cause the mandibular teeth to act in the manner of a melon-ball cutter and, if penetration was adequate, the crater wound would be completed.

To explore this possibility, I employed a nectarine (*Persicum* sp.) from the ship's galley since no large, dead fish was available at the moment. I pushed the teeth of a fresh, dead *Isistius* into the fruit and then rotated the body around that point. The result (Figure 4) was a neat, round, crater "wound" and the hemispheroidal "plug" in the shark's mouth with the small, hooked upper teeth securing it. If tooth penetration had been inadequate during such a sequence, the integument would be cut completely around but the plug would remain attached by a central peduncle. Necrosis of the plug would probably follow, resulting in conditions described by Mackintosh and Wheeler (1929). They presented a hypothetical sequence beginning with a crescentic wound which developed, by gradual erosion of the flesh, to the open pit stage. The "flabby" pedunculate plug, they believed, was a stage in the healing process and was sloughed off near the completion of healing.

They pointed out that the most obvious cause of crescentic and open pit wounds was the bite of some fish, but no fish known to them possessed teeth or a mouth structure which would produce such wounds. They, therefore, returned to the assumption that the wounds were a result of microbial infections.

Except in the cases of attacks on squids when the prey is killed, it appears that *Isistius*, in biting pieces out of living cetaceans and fishes, qualifies as a temporary parasite in the same sense that a mosquito does.

ACKNOWLEDGMENTS

I want to acknowledge the contributions of many persons who provided unpublished records, specimens of wounds and scars, photographs, as well as ideas and encouragement during the preparation of this manuscript. My special thanks are extended to John D. Fowler, Jr., NMFS, HAFRC, who initiated the important experiments at sea.

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7117

FORMATION OF A FALSE ANNULUS ON SCALES OF PACIFIC SARDINES OF KNOWN AGE

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Pacific sardines, *Sardinops caerulea* (Girard), were reared from hatching through the first year of life at the Fishery-Oceanography Center, La Jolla, California. The availability of these fish has allowed the study of growth in length and weight and the formation of accessory ring and annulus on scales of sardine of known age to compare with measurements of field-captured fish.

Sardine eggs were obtained on May 9, 1968, off San Diego, California. They were transferred to the Fishery-Oceanography Center aquarium and placed in a clear, thin-walled polyethylene bag which was suspended in sea water in a 3,500-gallon pool. The polyethylene bag, about 1 meter deep and 1 meter diameter, was used to confine the newly-hatched larvae to a small area of facilitate feeding. An air stone in the bag kept the water gently in motion. Light was constant, provided by a 1,000-watt mercury vapor lamp over the tank.

After 2 days between 16° and 18° C. the eggs hatched into larvae about 4 mm. long. The procedure of feeding changed as the fish grew. The larvae were fed a variety of wild plankton organisms, until the 11th day when their diet was supplemented with live brine shrimp, *Artemia salina,* nauplii. After 28 days the larvae were released into the pool. The food was changed to frozen brine shrimp and size #1 trout food at 52 days. During the first 2 months only a minimum amount of water was added to the pool periodically to flush off the surface scum. At the end of 2 months a constant flow of ambient sea water was maintained in the pool. At the beginning of the third month, the amount of food fed per day was set at 10 percent of the calculated total weight of the fish in the tank; a decision based on a study of food utilization by young anchovy, *Engraulis japonicus* (Temminck et Schlegel), by Takahashi and Hatanaka (1960). The average weight of the fish was obtained from monthly samples and the number of fish estimated until December when they were counted as they were being transferred to another pool.

The larvae were sampled frequently through the first 2 months (Figure 1) to obtain empirical data on their rate of growth. A total of 646 specimens were measured to the nearest half-millimeter SL during this period. From the third month on, samples were measured at 30-day intervals. The laboratory fish were smaller than fish obtained from the Pacific coast bait fisheries during the 1938–39 season (Walford and Mosher, 1943a) through November. After November their lengths were similar.

Two rings formed on the scales during the first year of life of the aquarium reared sardines (Figure 2). The first ring (accessory) formed between August and September 1968. The second ring (annulus) formed between December 1968 and January 1969. Both rings had all of the usual characteristics of an annulus. The second ring was considerably easier to see than the first ring.

Figure 3 illustrates several factors that may be related to formation of the rings. Formation of the accessory ring is associated with the period of maximum growth. Formation of the annulus ring occurs immediately prior to the onset of rapid growth during the late winter 1969. None of the other factors appear to be related to formation of the rings.

At the time of annulus formation the fish were about 7.5 to 8.5 months old and averaged 101 to 105 mm. SL, respectively. Back-calculated L_1 lengths on a random selection of scales from the December through March samples averaged 100.0 mm. SL. However, on their first actual birthdate the sardines averaged 124.5 mm. SL, nearly 25 percent greater actual observed length than their first year back-calculated length. At the time of the accessory ring formation the fish were about 4.5 to 5.0 months old and averaged 81.8 mm. SL.

Other investigators have reported two rings per year on scales taken from similar species. Aikawa (1940) reported that two rings formed on the scales of the Japanese sardines, *Sardinia melanosticta* (Temminck et Schlegel) per year. Davies (1958) found that two rings formed during the first year of life on scales taken from commercially caught South African pilchard, *Sardinops ocellata* (Pappe).

Formation of an accessory ring on scales of laboratory reared Pacific sardines during their first summer of life is cause for concern. If similar accessory rings form on scales of fish in their natural environment, considerable error in assigning ages to fish may result. Preliminary analysis of historical data and re-examination of previously read scales indicates that this type of error in aging has occurred. We are attempting to develop quantitative techniques for distinguishing between accessory rings and annuli.

ACKNOWLEDGMENTS

I am grateful to Andre Saraspe who deserves special credit for his successful effort in hatching and rearing the sardine larvae through their second month of life. Clark E. Blunt, James E. Hardwick, and John S. MacGregor did the scale reading. I wish to thank William H. Lenarz and Andrew M. Vrooman for

critically reviewing the manuscript. In addition, I wish to express my appreciation to Mary J. Kalin, Ruth Miller, and Nancy Wiley who helped measure the fish samples of the first 2 months, and to Pedro A. Paloma for caretaking duties during the writer's absences at various times.

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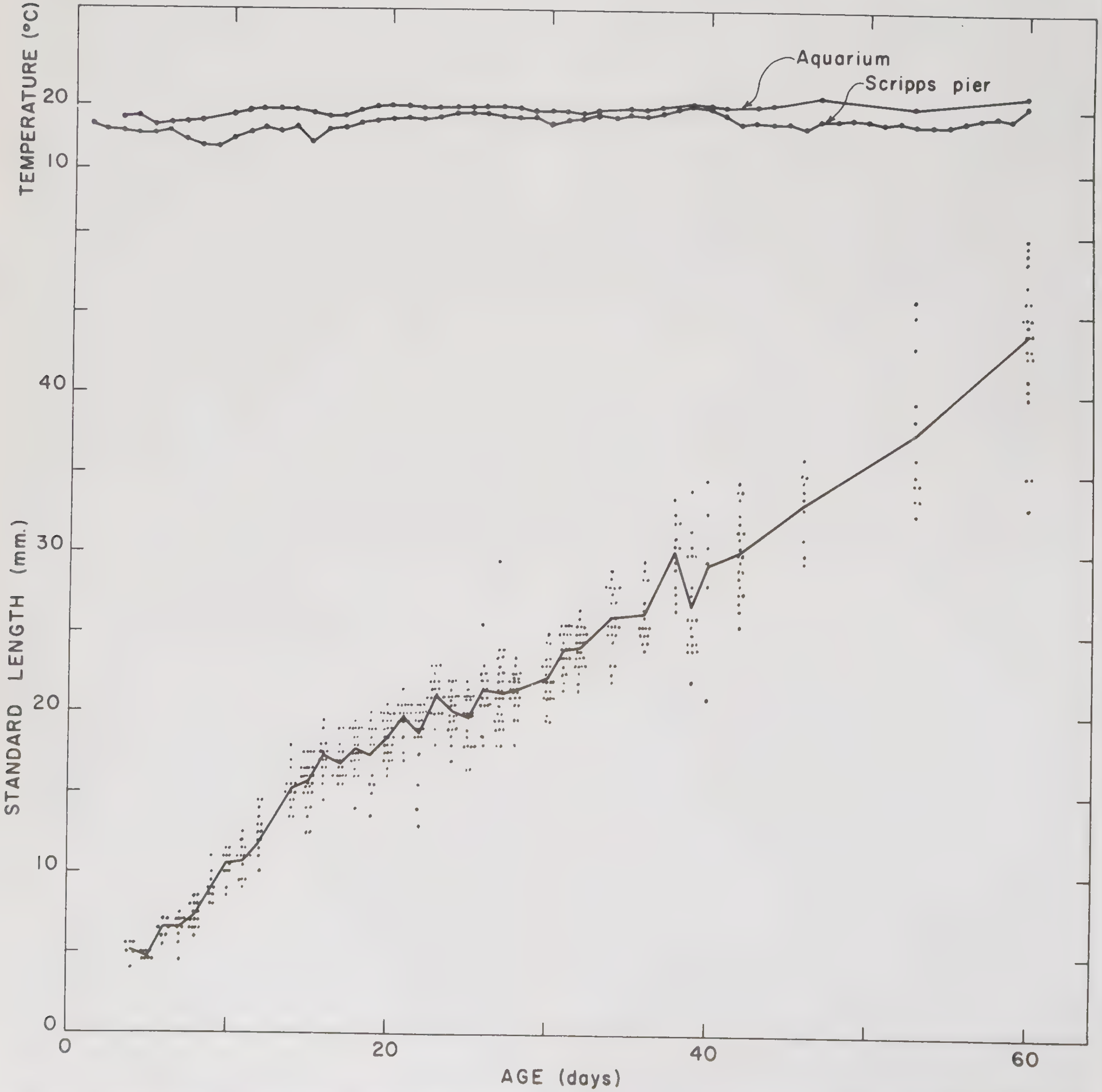

FIGURE 1. Standard lengths of the aquarium reared sardines during the first 2 months of life. The solid line connects the average lengths of the fish sampled on any one day. Scripps pier and the aquarium water temperatures are shown in the upper graph.

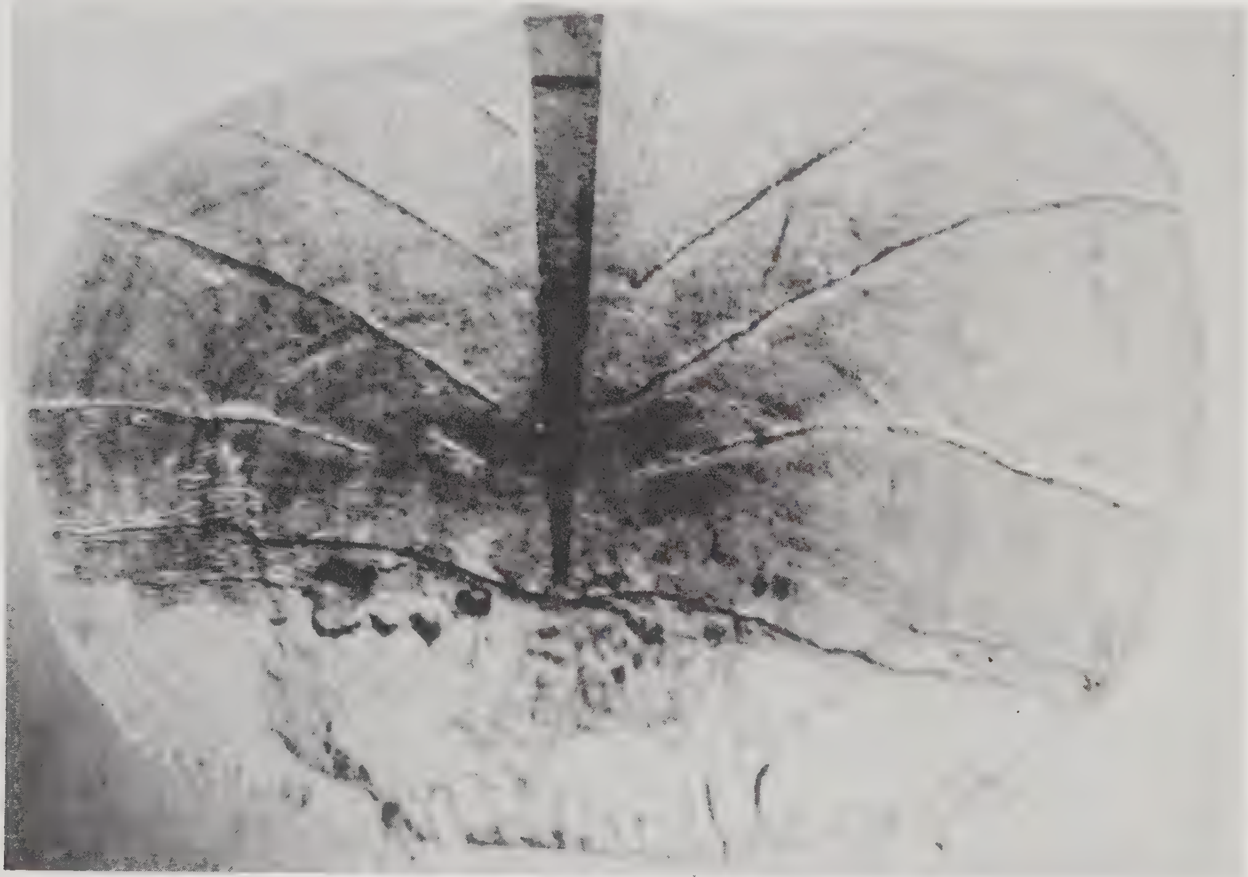

FIGURE 2. A typical scale from one of the aquarium reared sardines sampled in its tenth month of life, March 3, 1969. The dark marks drawn on the scales indicate the accessory check (inner mark) and the first annulus.

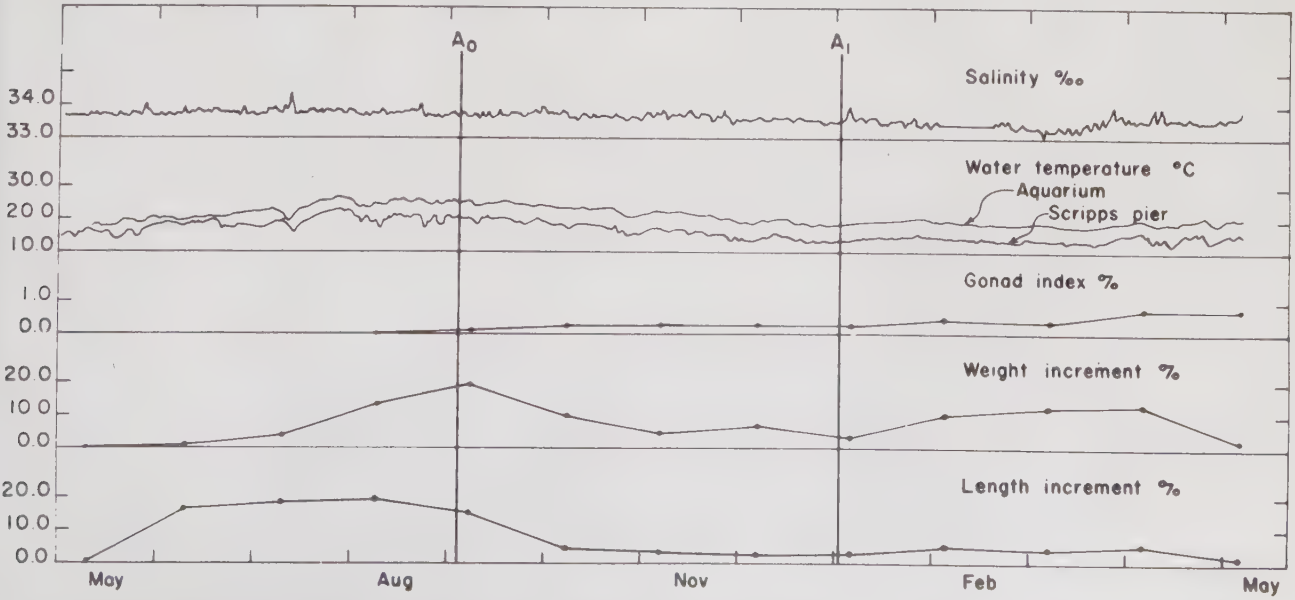

FIGURE 3. Average monthly length increment in percent of the average standard length at the end of 1 year, average monthly weight increment in percent of total weight at the end of 1 year, gonad index (weight of gonad in percent of body weight), along with water temperature and salinity. Periods of formation of the accessory check and the annulus are indicated by the vertical lines A_0 and A_1 respectively.

7118

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AGE COMPOSITION OF SARDINE LANDINGS ON THE PACIFIC COAST OF THE UNITED STATES AND MEXICO IN 1964–1965[1]

by

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California landings of Pacific sardines, *Sardinops caeruleus* (Girard), during the 1964–65 season amounted to 5,297 tons. During the interseason, 994 tons were landed.

Baja California sardine landings totaled 24,675 tons for this period, almost all of which came from San Sebastian Vizcaino Bay and Bahia de la Magdalena.

The age structure of the catch and low landings off California and northern Baja California reflect continued failure of the sardine population in the north to produce good year-classes.

INTRODUCTION

The rise and fall of the fishery for Pacific sardines is well known. Because of the continued interest in the sardine population and its apparent interaction with the northern anchovy, *Engraulis mordax* Girard, we continue to sample the landings for age and length composition.

Detailed reports of age and length composition of landings through the 1963–64 season have been reported in *California Fish and Game*. Beginning with the 1964–65 season, the reports will be abbreviated and follow the present format. A more detailed discussion of the sardine fisheries on the Pacific Coast of the United States and Mexico for 1964–65 and subsequent periods is available in various Marine Resources Region Reference Reports and may be obtained from the Marine Resources Region, 350 Golden Shore, Long Beach, California, 90802.

This report, the 19th of a series, summarizes the age composition of the 1964–65 period landings. We wish to acknowledge the assistance of John MacGregor, National Marine Fisheries Service; Harold Hyatt and Richard Wood, California Department of Fish and Game; and William W. Hatton, California Academy of Sciences.

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[1] Accepted for publication January 1971. This article was prepared in part while the junior author was working in cooperation with the Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, Project M-63-R.

TABLE 1—**Age and Year Class Composition of the Sardine Catch in the 1964–65 Season**

	Catch		Numbers of fish in thousands by age and year class								
			1	2	3	4	5	6	7	8	9
	Tons	Number	1963	1962	1961	1960	1959	1958	1957	1956	1955
Central California											
"August"[1, 2]	41	181	--	--	--	18	76	87	--	--	--
"September"[2]	118	511	--	--	--	15	157	213	126	--	--
"October"	57	321	64	141	13	--	--	45	58	--	--
"November"	14	65	--	5	2	--	22	27	9	--	--
"December"	68	308	--	24	41	35	31	57	78	14	28
"January"[3]	1	4	--	--	--	.6	.4	1.5	.8	.5	.2
"February"	5	19	--	--	--	3	2	7	4	2	1
"March"[4]	--	--	--	--	--	--	--	--	--	--	--
Total Central California	304	1,409	64	170	56	71.6	288.4	437.5	275.8	16.5	29.2
Percentage	--	99.99	4.54	12.07	3.97	5.08	20.47	31.05	19.57	1.17	2.07
Southern California											
"September"[5]	3,556	29,066	--	3,895	13,806	5,755	3,168	1,599	814	29	--
"October"	589	4,359	--	863	1,726	1,160	357	122	131	--	--
"November"	450	3,484	7	418	1,345	1,526	125	32	31	--	--
"December"	311	2,100	--	158	588	746	462	73	73	--	--
"January"	31	179	--	11	39	36	79	14	--	--	--
"February"[6]	4	27	--	--	7.3	11	7.2	.5	1	--	--
"March"[4]	52	296	--	--	80	122	80	4	10	--	--
Total Southern California	4,993	39,511	7	5,345	17,591.3	9,356	4,278.2	1,844.5	1,060	29	--
Percentage	--	100.00	.02	13.53	44.52	23.68	10.83	4.67	2.68	.07	--
Total California	5,297	40,920	71	5,515	17,647.3	9,427.6	4,566.6	2,282	1,335.8	45.5	29.2
Percentage	--	100.00	.17	13.48	43.13	23.04	11.16	5.58	3.26	.11	.07

Northern Baja California											
"September"[5]	38	236	--	--	21	97	104	14	--	--	--
"October"	215	1,449	--	--	406	609	319	72	43	--	--
"November"	899	5,784	--	--	983	2,892	1,678	231	--	--	--
"December"[7]	967	6,264	--	--	1,064	3,132	1,817	251	--	--	--
"January"[7]	262	1,698	--	--	289	849	492	68	--	--	--
"February"[7]	145	939	--	--	160	469	272	38	--	--	--
"March"[4, 7]	109	709	--	--	121	354	206	28	--	--	--
Total Northern Baja California	2,635	17,079	--	--	3,044	8,402	4,888	702	43	--	--
Percentage	--	100.00	--	--	17.82	49.20	28.62	4.11	.25	--	--
Central Baja California											
"September"[8]	651	5,510	--	309	1,435	1,899	1,391	397	88	--	--
"October"	1,363	11,436	--	640	2,974	3,934	2,882	823	183	--	--
"November"	775	6,500	--	182	1,378	2,392	2,288	130	130	--	--
"December"	970	8,117	--	349	1,567	3,060	2,167	869	105	--	--
"January"	734	6,489	--	260	2,660	1,492	1,493	584	--	--	--
"February"	1,439	12,056	--	--	1,929	6,028	2,170	723	1,206	--	--
"March"[4]	633	5,573	--	56	836	2,062	1,616	1,003	--	--	--
Total Central Baja California	6,565	55,690	--	1,796	12,779	20,867	14,007	4,529	1,712	--	--
Percentage	--	99.99	--	3.22	22.95	37.47	25.15	8.13	3.07	--	--
Total Baja California[9]	9,200	72,769	--	1,796	15,823	29,269	18,895	5,231	1,755	--	--
Percentage	--	100.00	--	2.47	21.74	40.22	25.97	7.19	2.41	--	--

[1] August 1–21.
[2] No samples; ages estimated from "July" sampling.
[3] No samples; ages estimated from "February" sampling.
[4] February 16–March 2 landings.
[5] September 1–20.
[6] No samples; ages estimated from "March" sampling.
[7] No samples; ages estimated from "November" sampling.
[8] No samples; ages estimated from "October" sampling.
[9] Includes Cedros Island and Ensenada only—2,847 tons from southern Baja California not sampled.

THE FISHERY

Fishing off California was poor with catches consisting primarily of sardines mixed with mackerel (jack mackerel, *Trachurus symmetricus,* and Pacific mackerel, *Scomber japonicus*). The age structure of landings for central and southern California (Table 1) reflected the continuing failure of the sardine population in the north to produce good year-classes.

In California the sardine season (also called the canning season) extends from August 1 through March 2 in central California (Pt. Arguello north) and September 1 through March 2 in southern California. The interseason for each area represents the period between successive seasons. Baja California landings are summarized on the same interseason and season basis.

During the interseason, California landings totaled 994 tons, with only 3 tons landed in central California. Season landings were 5,297 tons with 304 tons taken in central California and 4,993 tons landed in southern California. This brought the California total to 6,291 tons for the period March 3, 1964 to March 2, 1965.

The fleet off central California during the season consisted of two large (60 ft or over) and two small purse seiners and 12 lampara boats. The large purse seiners spent part of the season in southern California because of fish scarcity in central California. The fishermen were paid $65 per ton for sardines and $52.50 per ton for mixed sardines (30–70% sardines) and mackerel.

A total of 38 large purse seiners and 25 small purse seiners and lampara boats fished exclusively in southern California (two other large purse seiners from Monterey joined the southern California fleet during part of the season). One cannery in Oxnard and five in the Los Angeles-Long Beach area processed fish.

The sardine industry in Baja California has been processing a greater portion of the Pacific Coast catch in recent years. Sardine fishing here is permitted throughout the year; but for purposes of comparison with southern California catch statistics, the fishing period is divided into similar season and interseason periods.

Catches of sardines in the Ensenada (northern Baja California) area were insignificant. The bulk of sardines processed at Ensenada came from San Sebastián Vizcaíno Bay, which also provided fish for the cannery at Cedros Island (central Baja California). The cannery at Puerto Adolfo López Mateos (southern Baja California) was supplied with fish caught in Bahía de la Magdalena.

Season landings in the Ensenada, Cedros Island, and Puerto Adolfo López Mateos areas amounted to 12,047 tons (Table 1), and interseason landings amounted to 12,628 tons (Table 2). These landings (total) represent an increase of 27%, as compared to the 1963–64 period landings of 18,115 tons.

A total of 33 purse seiners and lampara boats fished in Baja California waters; 25 were based and landed catches at Ensenada, 4 at Cedros Island, and 4 at Puerto Adolfo López Mateos. Two of Ensenada's larger purse seiners equipped with refrigerated holds were based at Cedros Island during a part of the fishing season.

TABLE 2—**Age and Year Class Composition of the Sardine Catch in the 1964–65 Baja California [1] Interseason**

	Catch		Numbers of fish in thousands by age and year class							
			0	1	2	3	4	5	6	7
	Tons	Numbers	1964	1963	1962	1961	1960	1959	1958	1957
Northern Baja California										
"March"	244	2,797	--	--	895	503	504	699	196	--
"April"	134	1,499	--	--	445	474	58	193	279	--
"May"	148	2,141	--	364	1,263	514	--	--	--	--
"June"	214	2,531	202	339	1,522	354	84	--	--	--
"July"	873	9,758	781	1,307	5,982	1,366	322	--	--	--
"August"	511	5,197	--	--	--	729	2,183	1,663	--	624
"September"[2, 3]	5	52	--	--	--	7	22	17	--	6
Total Northern Baja California	2,129	23,925	983	2,010	10,136	3,945	3,173	2,572	475	630
Percentage	--	100.00	4.11	8.40	42.37	16.49	13.26	10.75	1.99	2.63
Central Baja California										
"March"[4]	598	4,738	--	--	569	2,085	1,611	473	--	--
"April"[4]	847	6,710	--	--	805	2,953	2,281	671	--	--
"May"	373	3,020	--	--	362	1,329	1,027	302	--	--
"June"[4]	370	2,999	--	--	360	1,320	1,019	300	--	--
"July"	1,130	9,450	--	--	567	3,591	4,158	851	283	--
"August"	1,185	9,188	--	--	478	1,691	3,932	1,874	1,213	--
"September"[2]	54	427	--	--	24	111	147	108	37	--
Total Central Baja California	4,566	36,532	--	--	3,165	13,080	14,175	4,579	1,533	--
Percentage	--	99.99	--	--	8.66	35.80	38.80	12.53	4.20	--
Total Baja California	6,695	60,457	983	2,010	13,302	17,025	17,348	7,151	2,008	630
Percentage	--	100.00	1.63	3.32	22.00	28.16	28.70	11.83	3.32	1.04

[1] Includes Cedros Island and Ensenada only—5,933 tons from southern Baja California cannery not sampled.

[2] August 22–September 1 landings.

[3] No samples; ages estimated from "August" sampling.

[4] No samples; ages estimated from "May" sampling.

Five canneries operated in the Ensenada area, one on Cedros Island, and one at Puerto Adolfo López Mateos. The domestic demand for canned sardines was good and the price to the fishermen ($32–$42/ton) fluctuated very little with $40 per ton being the average price paid during the 1964–65 period.

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SEASONAL AND GEOGRAPHIC CHARACTERISTICS OF FISHERY RESOURCES

California Current Region--IV. Pacific Mackerel

David Kramer and Paul E. Smith

The fishery for the Pacific mackerel (Scomber japonicus) was until 1936 the third largest in southern California, surpassed only by those of the Pacific sardine and tuna. This mackerel has declined until, in 1970, a 2-year moratorium was implemented by the California Legislature in an attempt to conserve the remainder of the resource and to assist in its revival.

Unlike our previous reports in this series (Kramer and Smith, 1970a, b, c), which briefly discuss the potential for each of the fisheries described, this deals only with the seasonal and geographic characteristics of the Pacific mackerel resource and describes briefly its decline and the result.

Summerized data (1951-60) for the Pacific mackerel from the collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) show that the major centers of spawning (10% or more occurrences of larvae in standard plankton tows) appear first in January in a small, inshore area south of Point Eugenia, Baja California (Figure). (The organizations, area of investigations, and treatment of the data were reported by Kramer and Smith, 1970a). The extent of the spawning centers remains small in this area with a trend of spawning northward--in 5% or more occurrences of larvae--until April, when the major centers extend farther offshore and to areas off northern Baja California. Finally, in May, the centers of spawning appear off southern California and, by July, extend a considerable distance offshore and north of Point Conception. Later, by October, the centers are found only off central Baja California. (Data for August, September, November, and December in the decade are insufficient for summarization to show the trends depicted in figure.)

Its Range

The Pacific mackerel once ranged from southeast Alaska (Rounsefell and Dahlgren, 1934) to Banderas Bay, Mexico (John E. Fitch, California Department of Fish and Game--CF&G--correspondence). CalCOFI data on mackerel larvae (Kramer, 1960, 1969) indicate that the spawning populations extend only as far north as Point Conception, California. Richard E. Parrish (CF&G, correspondence) has reported repeated traces of Pacific mackerel taken with jack mackerel off Pt. Sur, California. Data on larvae indicate that the Pacific mackerel extends southward along the coast and into all of the Gulf of California. Larvae found by the CalCOFI (Ahlstrom, 1956) at the mouth of the Gulf indicate that the resource may extend at least to Banderas Bay, as reported by Fitch.

Tagging Program 1935-1943

In 1935-43, a tagging program was carried out by CF&G (Fry and Roedel, 1949) in order to understand the movements of the mackerel and determine to what degree the populations from other areas (Roedel, 1952) contributed to the major fishery off southern California. Mackerel were tagged throughout their range--by the Fisheries Research Board of Canada off the Columbia River, and by CF&G from central California to San Roque Bay, about half way down Baja California. Tag returns showed that there was an interchange of fish throughout the region covered by the program, and that all regions contributed to the southern California area.

Decline of Fishery

Blunt and Parrish (1969) reported that this major California fishery, which reached a

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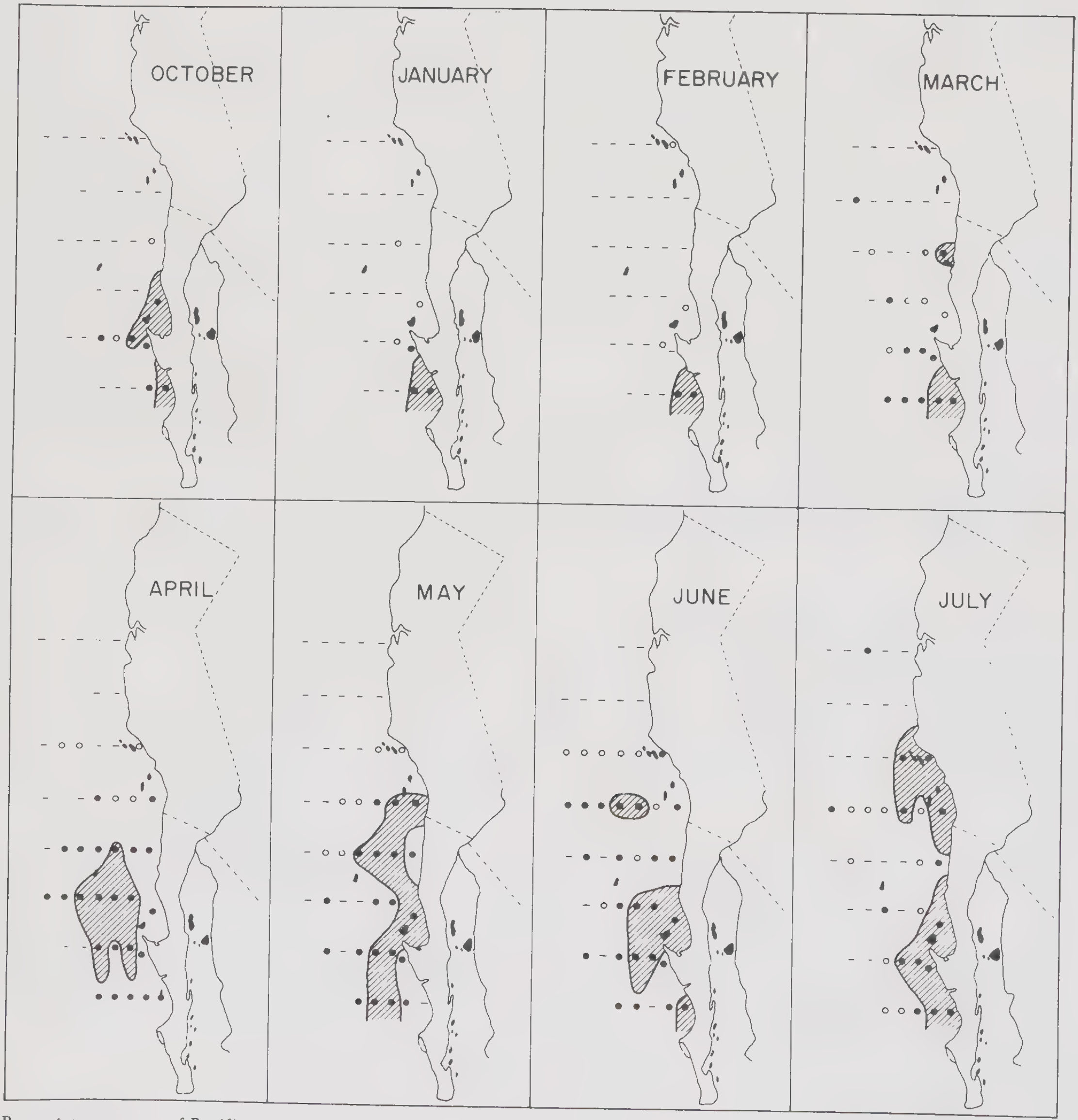
OCTOBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY

Percent occurrences of Pacific mackerel larvae in 1951-60 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each line, circle or dot represents a pooled statistical area (see Kramer and Smith, 1970a). (o)--less than 5% occurrence; (●)--equal to or greater than 5% occurrence; shaded area--equal to or greater than 10% occurrence; (-)--area occupied with no occurrence.

peak catch of 73,000 tons in 1935, had declined to record low catches of 583 tons in 1967 and 1,565 tons in 1968. Also, that in Baja California the catch had been declining since 1963 and, in 1968, had dropped to 1,334 tons. This decline is reflected in part by our summarized data for 1951-60, where "high" abundance of spawning populations are indicated by 10% or more occurrences of larvae. (Our previous reports on relatively abundant fishes used 49% for jack mackerel, 20% for Pacific saury, and 50% for Pacific hake.)

Blunt and Parrish estimated the present spawning biomass of Pacific mackerel at less than 5,000 tons. They stated further that "Certain environmental factors detrimental to good recruitment are indicated and if this continues through 1969, long term loss of the fisheries is a distinct possibility." In 1969, California landings were 1,178 tons; no figures are available for Baja California landings for that year.

Legislature Acts

On March 31, 1970, the California legislature passed a bill providing that "Pacific mackerel may not be taken or possessed at any time for any purpose except loads or lots of fish may contain 18% by weight of Pacific mackerel taken incidentally to other fishing operations. Such Pacific mackerel, incidentally taken, may be used for any purpose." This is a 2-year act to ". . . remain in effect only until the 61st day after adjournment of the 1972 Regular Session."

On August 14, the Governor of California signed the bill into law. It will go into effect on November 25, 1970.

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Pacific Mackerel

7120

SEASONAL AND GEOGRAPHIC CHARACTERISTICS OF FISHERY RESOURCES

California Current Region--V. Northern Anchovy

David Kramer and Paul E. Smith

The resource of the northern anchovy, Engraulis mordax, off the coasts of California and Baja California has been estimated to have grown from 640,000 tons in 1951 to a spawning biomass fluctuating between 5 and 8 million tons since 1962 (Smith, MS). (Estimates from various sources, 1940-41 to 1965, were compiled by Messersmith in 1969--Table 2.) The growth has been attributed, in part, to the anchovy's occupation of the niche left empty by the Pacific sardine during its decline. In 1966, Ahlstrom depicted this phenomenon in comparing the relative abundance and distribution of the larvae of the two species for 1954 and 1962 (Figs. 1 and 2). Data from fossil scales, presented by Soutar (1967) and Soutar and Isaacs (1969), offer an alternate explanation to the anchovy's filling the sardine's niche. They imply that fluctuations in the populations of these two species may have been independent of one another in different periods over the last 2,000 years.

In 1964, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Committee proposed to the California Marine Research (MRC) Committee that a 200,000-ton harvest be allowed for reduction purposes on the hypothesis that a fishery for this species might help to restore the sardine resource; once restored, proper management could maintain a balance between the two resources. This was detailed by Messersmith in 1969.

Seasonal and Geographic Distribution

Two sources of information are available on the seasonal and geographic distribution of the anchovy population. One is a tagging study in 1966-69: the California Department of Fish and Game (CF&G) tagged anchovies from San Francisco, California, to Ensenada, Baja California, to determine their migratory habits and to obtain estimates of their population size and mortality rates (Haugen, Messersmith and Wickwire, 1969). Recoveries of tags indicated northerly movement during late summer and southerly movement during the winter. The data were insufficient to determine the sizes of the population mortality rates, or total distribution, because of the low level of the reduction fishery during that period of the study and lack of catch statistics south of Ensenada.

Vrooman and Smith (MS), using serological data, estimated the same movements in a central subpopulation of the anchovy between Pt. Conception, California, and Cedros Island, off Baja California. This subpopulation is included in the area depicted by Haugen, et al. (1969) for their tagging work.

The second source are the data of the CalCOFI, which show the seasonal and geographic distributions of anchovy larvae, cruise by cruise, for 1951-65 (Kramer and Ahlstrom, 1968), and in summaries for eggs and larvae for 1951-60 (Figs. 3 and 4) over the full range of the investigations.

Summarized data can be used to predict the times and locations of adult fish spawning as described by Kramer and Smith (1970a) in the first report in this series, where the organizations, area of investigations, and treatment of the data were presented.

Unlike our previous reports, which used either all eggs or all larvae for the summaries (Kramer and Smith, 1970a, b, c, d), we are using both for the anchovy; for the larvae, we are using the 5-mm size only, the most abundant in the plankton hauls.

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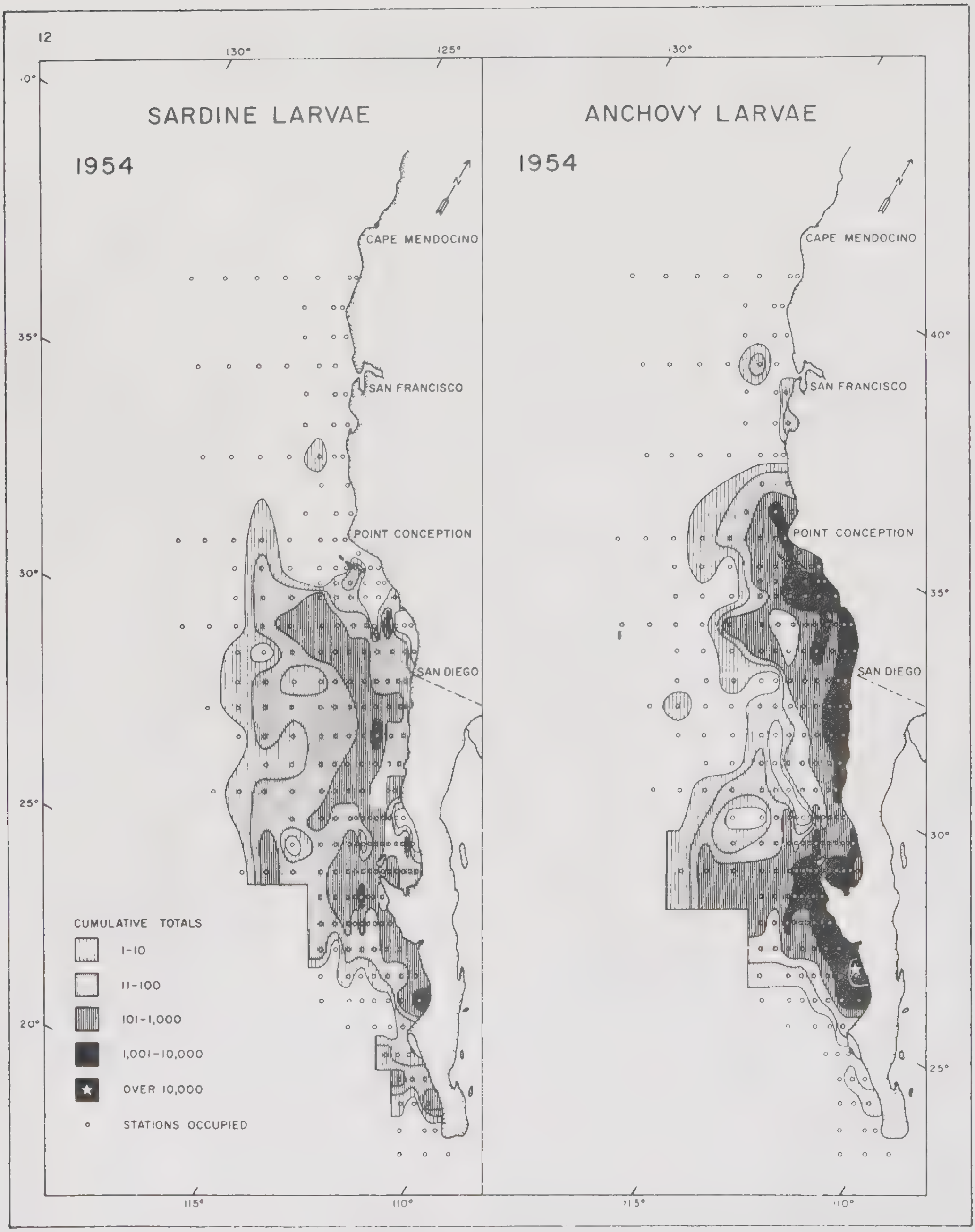
12
SARDINE LARVAE
1954
ANCHOVY LARVAE
1954
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
130°
125°
115°
110°
40°
35°
30°
25°
20°
CUMULATIVE TOTALS
1-10
11-100
101-1,000
1,001-10,000
OVER 10,000
STATIONS OCCUPIED

Fig. 1 - Distribution and relative abundance of sardine and anchovy larvae in 1954 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). (Fig. 2 of Ahlstrom, 1966.)

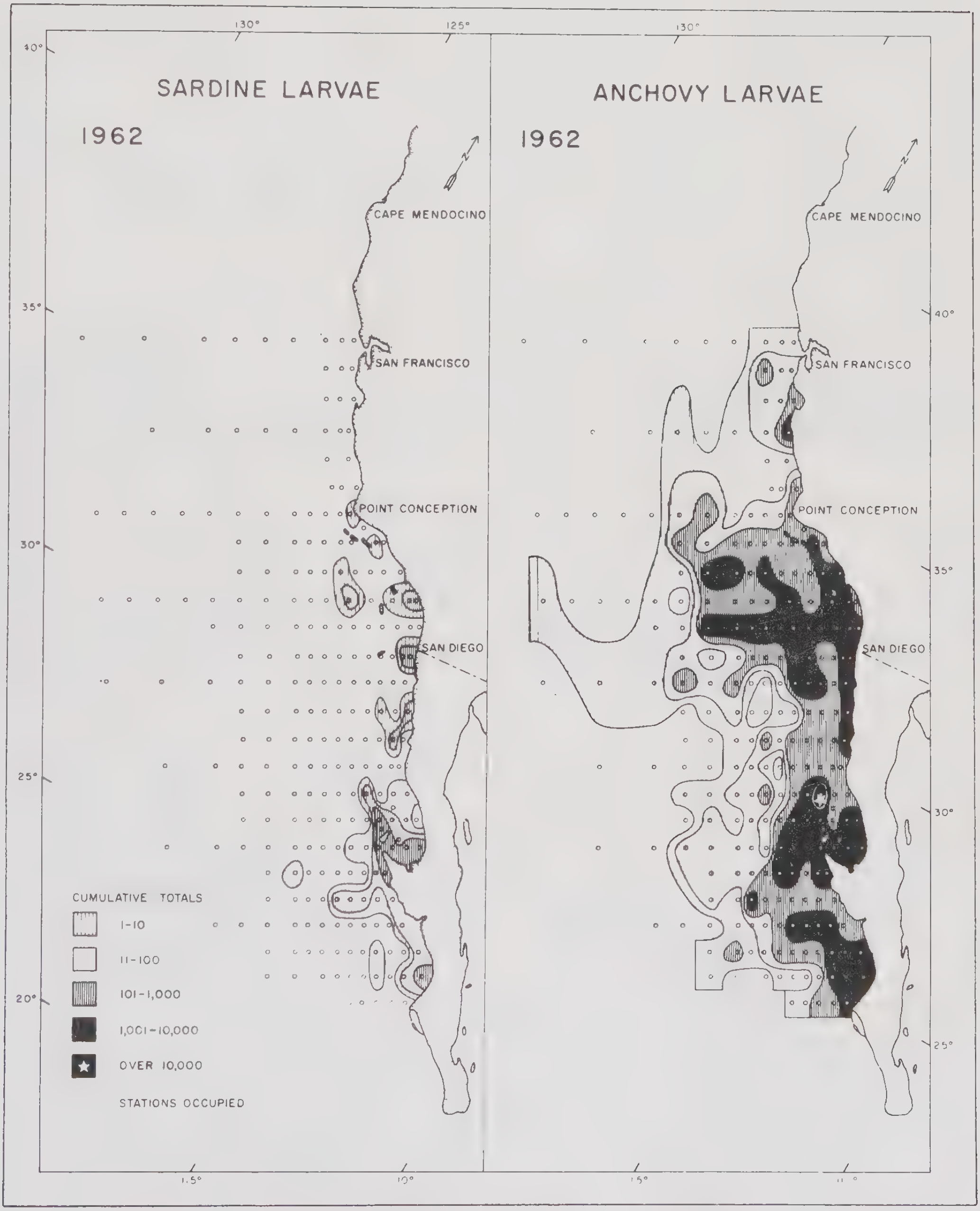
SARDINE LARVAE
1962
ANCHOVY LARVAE
1962
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
N
130°
125°
40°
35°
30°
25°
20°
CUMULATIVE TOTALS
1-10
11-100
101-1,000
1,001-10,000
OVER 10,000
STATIONS OCCUPIED

Fig. 2 - Distribution and relative abundance of sardine and anchovy larvae in 1962 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). (Fig. 3 of Ahlstrom, 1966.)

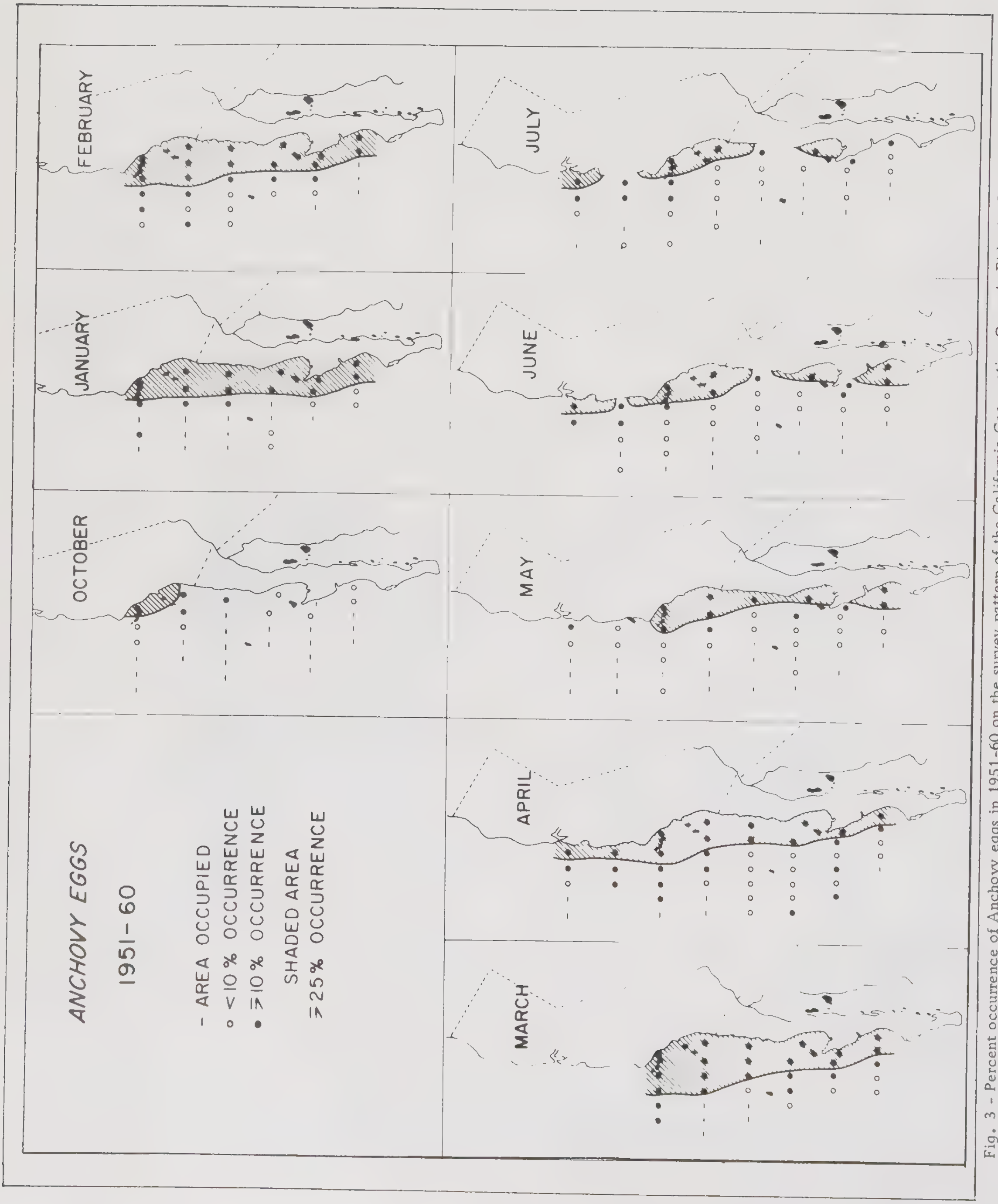
ANCHOVY EGGS
1951-60
- AREA OCCUPIED
○ <10% OCCURRENCE
● ≥10% OCCURRENCE
SHADED AREA ≥25% OCCURRENCE
FEBRUARY
JANUARY
OCTOBER
JULY
JUNE
MAY
APRIL
MARCH

Fig. 3 - Percent occurrence of Anchovy eggs in 1951-60 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each circle, line or dot represents a pooled statistical area (see Kramer and Smith, 1970a).

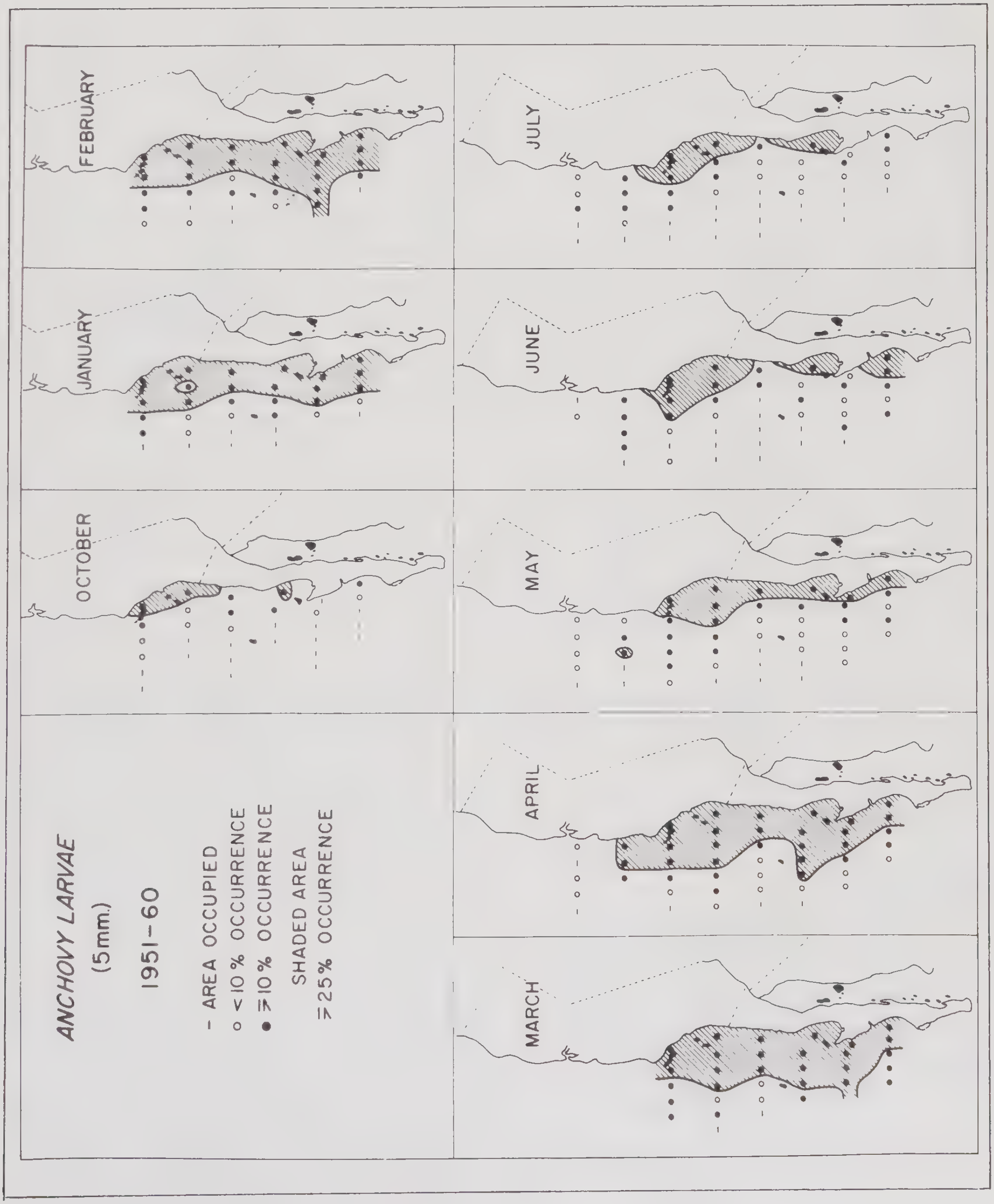
ANCHOVY LARVAE
(5mm.)
1951-60
- AREA OCCUPIED
○ <10% OCCURRENCE
● ≥10% OCCURRENCE
SHADED AREA
≥25% OCCURRENCE
OCTOBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY

Fig. 4 - Percent occurrence of 5-mm anchovy larvae in 1951-60 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each circle, line or dot represents a pooled statistical area (see Kramer and Smith, 1970a).

The eggs and larvae show only slight differences in the extent of their distributions in the same month for which each is shown. The major centers of spawning (25% or more occurrences in plankton hauls) are evident first in January from Pt. Conception, California, to Pt. San Juanico, Baja California, and about 50 miles seaward. The north to south extents remain the same through April, with some increase seaward and northward to San Francisco. The southern extent remains the same in May, June, and July, but the northern limit varies between Pt. Conception and San Francisco. By October, the centers are located only off southern California and sometimes southward. The data for August, September, November, and December were insufficient for summarization to show the trends depicted in Figs. 3 and 4.

The Fishery

Until the 1965-66 season, when a reduction fishery was allowed by the California Fish and Game Commission for the northern anchovy in California, the resource had been virtually untapped. Major usage was in commercial landings restricted to canning and in landings for live and dead bait. Total use, including the new fishery for reduction, was summarized by Messersmith (1969) in his review of the industry through 1967, and by Hardwick (1969) for the fishery through 1968.

Landings for reduction have been strictly limited and controlled by the California Fish and Game Commission to quotas by zones and areas along the California coast with some slight changes from year to year (Messersmith, 1969; Hardwick, 1969). Quota totals were 75,000 tons for each season, 1965 through 1969. The quota total was raised to 100,000 tons for the 1970-71 season. Anchovy landings 1964 through 1969 are shown in Table.

Anchovy landings 1964 through 1969
(source - California Department of Fish and Game)

Year	Reduction	Other commercial	Live bait	Total
1964	0	2,488	5,191	7,679
1965	170	2,866	6,148	9,184
1966	27,335	3,705	6,691	37,731
1967	32,349	2,455	5,387	40,191
1968	13,795	1,743	7,176	22,714
1969*	65,099	2,533	5,538	73,170

*Preliminary.

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7121

SEASONAL AND GEOGRAPHIC CHARACTERISTICS OF FISHERY RESOURCES

California Current Region - VI. Rockfish

David Kramer and Paul E. Smith

The purpose of this report on the rockfish resource, family Scorpaenidae, as for others in this series (Kramer and Smith, 1970a,b,c,d, 1971), is to describe the seasonal and geographic characteristics of their spawning populations on the basis of summarized data on the abundance of their larvae in the decade 1951-60. The organizations, area of investigation, and treatment of the data were presented in the first report of the series.

The rockfishes of the northeast Pacific are of major importance in the commercial and sport fisheries of the United States (Phillips, 1957, 1958). The family consists of so many species, most of them in the genus Sebastes, that they are usually grouped only under the common name "rockfish" in the commercial landing reports of the State of California. The family consists of three genera, of which Sebastes has at least 55 species; Sebastalobus has two species, and Scorpaena one. In California, three species of Sebastes comprise the major portion of the commercial catch of rockfish for human consumption, about six species form the greatest part of the animal food fishery, and two contribute chiefly to the sport fishery. The single species of Scorpaena contributes to both the commercial and sport fisheries. The California fisheries and others in the northeast Pacific are described briefly at the conclusion of this report.

Sebastes Most Abundant Genus

The most abundant genus in the rockfish larva collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) is Sebastes which, until recently, has been enumerated only as "rockfish", with no differentiation to species. Our knowledge of adult spawning, therefore, is based on total rather than individual species distributions. Some species, and the times and locations of their spawning, are discussed below.

The rockfish family in the northeast Pacific extends from the Gulf of Alaska to Baja California (Phillips, 1957; Ahlstrom, 1961). The CalCOFI surveys have delimited the distributions of rockfish larvae to their southernmost extent and offshore off almost all of Baja California as indicated in the figure. They have not delimited the populations seaward off California nor in their northernmost extent where, in the limits of the surveys, they have been found as far offshore as 250 miles and as far north as the California-Oregon border.

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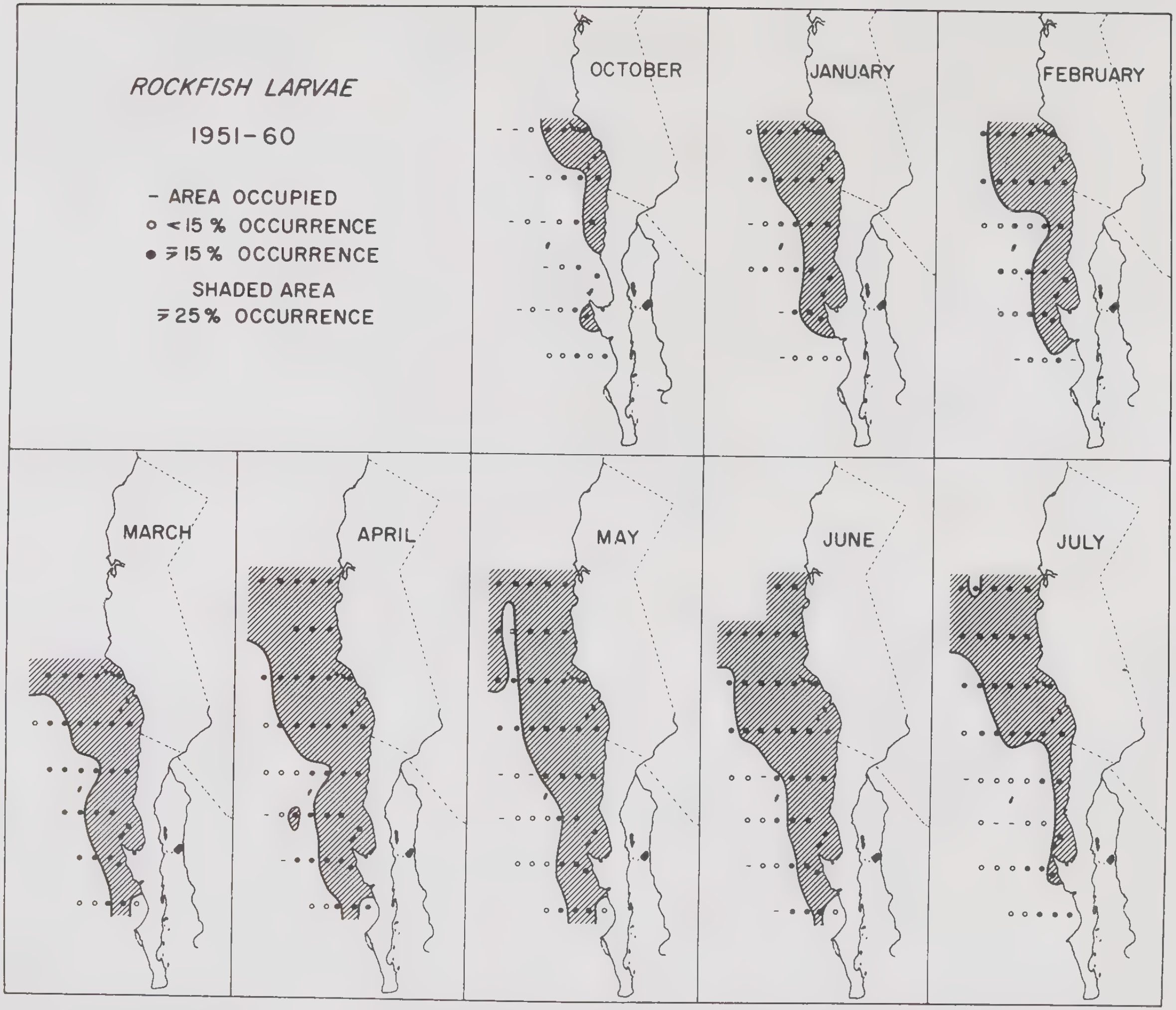
ROCKFISH LARVAE
1951-60
- AREA OCCUPIED
○ <15 % OCCURRENCE
● ⩾15 % OCCURRENCE
SHADED AREA
⩾25 % OCCURRENCE
OCTOBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY

Percent occurrence of rockfish larvae, Sebastes spp. in 1951-60 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each circle, line or dot represents a pooled statistical area (see Kramer and Smith 1970a).

Plankton data on rockfish are for larvae only. Their eggs are not planktonic because the genus Sebastes is ovoviviparous--the female is externally fertilized and incubates the eggs until the young are born upon extrusion into the water (Phillips, 1958). The genera Sebastalobus and Scorpaena lay their eggs in gelatinous floating masses (Pearcy, 1962; Phillips, 1958) which, to our knowledge, have never been collected in CalCOFI tows.

Summarized data for 1951-60, January through March, are for the area from Point Conception, California, to Point San Juanico, Baja California. The major centers of spawning (25 percent or more occurrences of larvae in plankton hauls) are delimited seaward in the survey pattern but not by the northernmost extent of the surveys. The areas of major spawning are about the same during those months with a slight spread seaward with time. Most of the surveys in April through July extended northward to the areas off San Francisco. In these months, the spawning centers extended farther seaward off southern and central California but were not delimited seaward or northward.

Definitive Spawning Periods

Recent identifications of some species of rockfish larvae collected on a number of CalCOFI surveys indicate that species or species groups have definitive spawning periods and geographic ranges. The chilipepper, Sebastes paucispinis, and shortbelly, S. jordani, are early-year spawners off southern and central California (unpublished data). The coral-red, S. macdonaldi, is a spring spawner with greatest numbers occurring off Baja California from Cape Colnett to Punta San Juanico (Moser, in press). The rosy, S. rosaceus group, is a summer spawner with a southern distribution off Baja California. This latter group is related to the few species of Sebastes off the coast of Chile; from this it has been hypothesized that the group, at one time, may have formed a continuous population from North to South America (personal communication, E. H. Ahlstrom, Fishery-Oceanography Center, NMFS, La Jolla, California).

The narrowing of the offshore band of spawning centers off Baja California in July, and the separation of centers in October[1], may be indications of spawning by species, species groups, and/or subpopulations. Data are not sufficient yet to form definite opinions on these points. Barrett, Joseph, and Moser (1966) in a study on the analysis of blood groups of the genus Sebastes (= Sebastodes) clarified a differentiation of species pairs which lends support to their distinction as species.

The Fisheries

The California Department of Fish and Game reports three kinds of fisheries in which different species of Sebastes are most dominant (Frey, 1971). The first, from Eureka to Santa Barbara, is for animal food in which unmarketable, trawl-caught rockfish are ground whole and quick-frozen for use on fur farms. Their important species are splitnose, S. diploproa, darkblotched, S. crameri, stripetail, S. saxicola, greenstriped, S. elongatus, sharpchin, S. zacentrus, and greentail, S. chlorostictus.

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[1] Data for August, September, November, and December are insufficient for summarization to depict the trends shown in the figure.

The second is the commercial fishery for fresh food to which only three species, caught chiefly by trawl, contribute the greatest catches from Eureka to Santa Barbara. These are bocaccio, S. paucispinis, canary, S. pinniger, and chilipepper, S. goodei.

The third is the sport fishery dominated by the blue, S. mystinus, and olive, S. serranoides. The sculpin, Scorpaena guttata, contributes abundantly to the fresh food fishery, chiefly by set lines, and the sport fishery.

Although little is known about the status of the rockfish populations, most of the catches remain good with no evidence of reduction by any particular pressures. The California Department of Fish and Game estimates that a sustained yield of 15 to 20 million pounds could be maintained off California (Frey, 1970).

Some of the rockfish species important to the California fishery also figure significantly in the Washington and Oregon catches (Alverson, Pruter, and Ronholt, 1964). These are boccacio, canary, and chilipepper. The major contributor in that commercial catch is the rockfish, S. alutus, marketed as Pacific ocean perch. Others include blackthroat, S. aleutianus, silvergray, S. brevispnis, yellowtail, S. flavidus, black, S. melanops, and flag, S. rubrivinctus.

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7122

SEASONAL AND GEOGRAPHIC CHARACTERISTICS OF FISHERY RESOURCES

California Current Region--VII. Pacific Sardine

David Kramer and Paul E. Smith

The fishery for the Pacific sardine, Sardinops caeruleus, was, during the 1930s and early 1940s, the largest in the western hemisphere; it produced nearly 25% of all fish caught in the United States.

Research on this resource had been going on for about 25 years, when its decline in the 1940s triggered the most intensive fishery study ever mounted in the world--the California Cooperative Oceanic Fisheries Investigations (CalCOFI). During the decade 1951-60, surveys were carried out each year almost on a monthly basis. Their data have been used as a base for analysis of the sardine and other pelagic resources in the California Current region. For this series of reports, the data have been used to summarize trends in densities of spawning populations by season and geography off the coasts of California and Baja California (Kramer and Smith, 1970a, b, c, d, 1971a, b). The agencies of the CalCOFI, their area of survey, and the methods of treating the data were described in our first report.

One reason given for the decline of the sardine was the intensive fishing pressure brought on by the profitable reduction of whole fish to meal and oil; from 1936 through 1945, tonnage for reduction exceeded tonnage for canning. Landings reached a high of 791,000 tons in the 1936-37 season and, from 1937-38 through 1944-45, fluctuated from 493,000 to 680,000 tons. The northern fishery off Canada, Washington, and Oregon was one of pressure on older fish that migrated from the subpopulations off California. The northern fishery collapsed as intensive fishing off California reduced the age structures of the sardine populations on that coast. In a population biology study of this species, Murphy said in 1966 that the pre-1949 population had a maximum sustainable yield of 471,000 tons at a spawning population of 1 million tons.

As reported by the California Department of Fish and Game (Frey, 1971), sardine numbers in the variable environment of the California Current region were dependent on an age structure which contained seven or eight significant reproductive classes. The intensive fishery lowered sardine life expectancy so that the population began to approach single-class reproduction. Thus, with its inherent resiliency stripped away, the northern subpopulation (off central California) collapsed following two highly unsuccessful spawnings in 1949 and 1950.

In our report on the northern anchovy (Kramer and Smith, 1971a), we discussed briefly two other possible reasons for the failure of the sardine to recover its former abundance. One was the taking over of the sardine's ecological niche by the anchovy; the other was the possibility of natural fluctuation wherein the two species may have been independent of one another in different periods over the last 2,000 years (Soutar, 1967; Soutar and Isaacs, 1969).

Seasonal and Geographic Distributions

At one time the sardine ranged from southern Alaska to the Gulf of California. Tagging studies (Clark, 1945) conducted by Canada and the States of Washington, Oregon, and California (California also tagged sardines off central Baja California) indicated that the fish moved from every region to all of the others. Returns from those tagged on Baja California showed migration northward only as far as southern and central California.

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COMMERCIAL FISHERIES REVIEW
Reprint No. 922

Attempts to differentiate subpopulations have been made on the basis of 1) differences in vertebral counts (Clark, 1947; McHugh, 1950)--indicating heterogeneity but not necessarily significant differentiation; 2) differences in temporal and areal spawning (Ahlstrom, 1960)--indicating fairly distinct subpopulations, "northern" off California and northern Baja California, "southern" off central Baja California, and "gulf" in the Gulf of California. (These differences can be seen in a 1970 atlas by Kramer which depicts the relative abundance of sardine eggs and larvae collected on every survey by the CalCOFI from 1951 through 1966); and 3) differences in blood systems (Sprague and Vrooman, 1962; Vrooman, 1964) which substantiated those subpopulations of Ahlstrom's analyses. The serological studies further demonstrated the movements evidenced by the tagging studies. These showed northern and southern subpopulations moving northward in spring and summer, and south in fall and winter.

Summarized data for 1951-60, used to predict the times and locations of adult sardine spawning, are shown in Figures 1 and 2. The relative distributions of all eggs and larvae collected by the CalCOFI for all cruises from 1951 through 1966 were depicted in an atlas by Kramer (1970). As for the anchovy (Kramer and Smith, 1971a), the summarized data on eggs and larvae are used to depict the occurrences for January through July and for October. The distributions for 5-mm larvae only are used because they are most abundant in plankton hauls.

Eggs and larvae show only slight differences in extent of their distributions in each of the same months for which they are illustrated. The lack of similarly shaded areas, for larvae as for eggs, 20% or more occurrences in plankton hauls, is attributed to the escapement, not absence, of small larvae through the meshes of the standard 1-m CalCOFI net (personal communication, William H. Lenarz, NMFS, La Jolla, California). The major centers of spawning (shaded areas) are evident first in January in small areas off central Baja California and southern California. These are the northern and southern subpopulations described above. With the passage of time, the southern group spreads northward and seaward; then, in May and June, it intermixes with the northern group, which spreads somewhat southward. In July, the two groups are separate again and, in October, heavy spawning occurs only off central Baja California. This is the off-season spawning group described by Ahlstrom (1960, p. 420), which he defined as the southern subpopulation.

The Fishery

The California Department of Fish and Game, in its report on the State's living marine resources (Frey, 1971), concluded its history of the sardine fishery: "Prior to 1967, management of the sardine resource in California almost entirely was limited to (1) control of tonnage of whole fish used for reduction, (2) case pack requirements (set number of cases of canned fish per ton of whole fish), and (3) restriction of the fishing season to the time of year when fish were most available and in prime condition for processing. A moratorium on sardine fishing in California was in effect during the 1967-68 and 1968-69 seasons. The moratorium limited the quantity of sardines which could be taken incidentally with other fish to 15% by weight of a mixed load. California landings for the 1967-68 season were 71 tons, while 52 tons were landed during the 1968-69 season.

"An extremely lucrative bait market for sardines has developed in the San Francisco Bay area in recent years. Sardines landed in California for this market bring the fishermen $400 to $500 per ton. During 1968, there were 323 tons of sardines imported from Mexico for use as bait. A bill (AB 564) enacted by the California Legislature in 1968 permitted the taking of 250 tons annually for bait. At present, the San Francisco-Delta bait market appears to be the most significant economic factor responsible for continued fishing mortality of the California sardine resource."

In its final discussion on the pelagic wetfish (packed in a "wet" condition, then cooked--hence wetfish), the Department stated:

"Landings of pelagic wetfish have been sizable in the past but have declined in more recent years. This decline is due to several factors: (1) the decline of sardine and Pacific mackerel stocks; (2) prohibiting the fishing industry from harvesting abundant anchovy stocks at a level indicated reasonable by scientific evidence; and (3) failure of the fishing industry to harvest greater

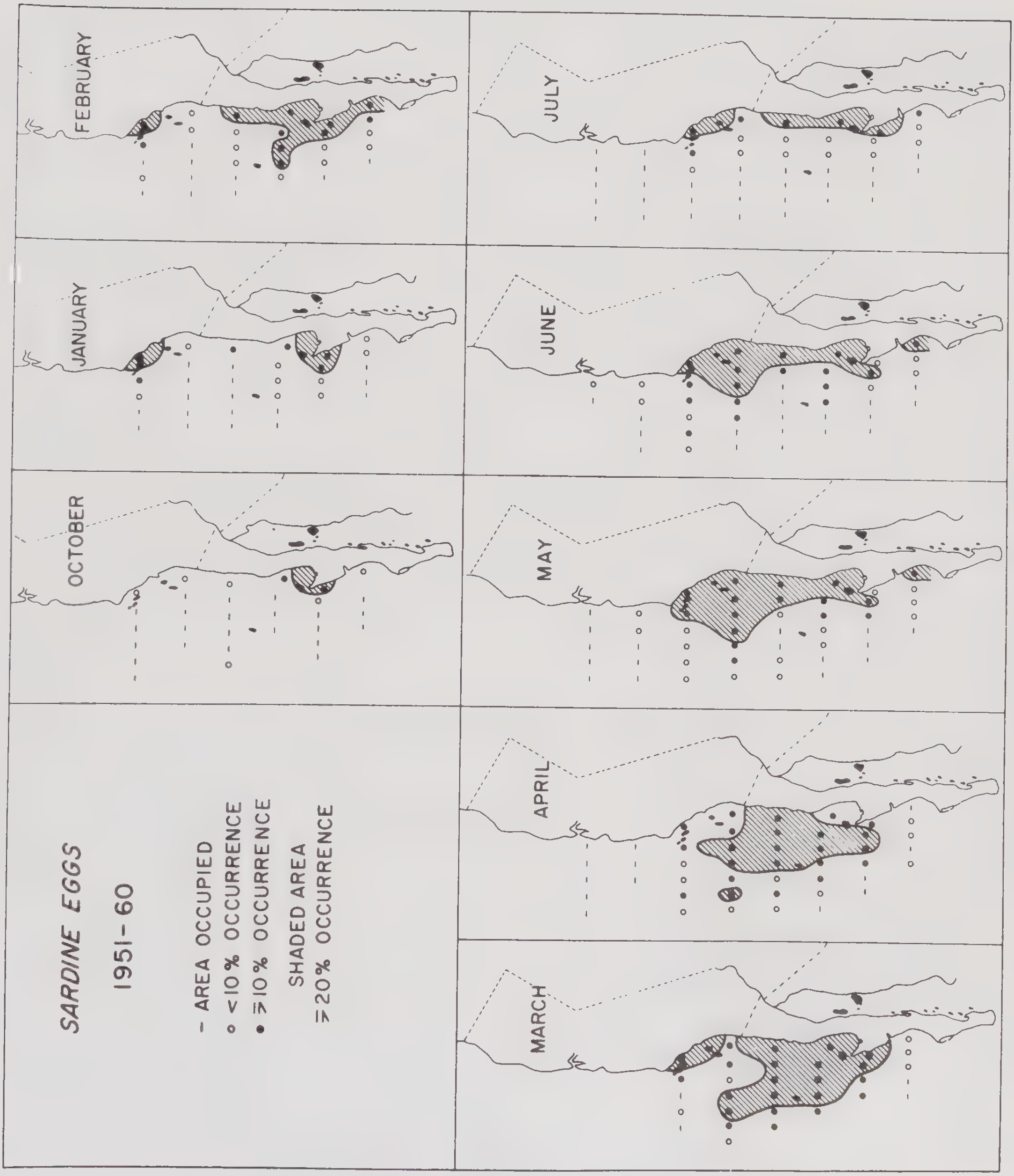
SARDINE EGGS
1951-60
- AREA OCCUPIED
○ <10% OCCURRENCE
● ⩾10% OCCURRENCE
SHADED AREA
⩾20% OCCURRENCE
OCTOBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY

Fig. 1 - Percent occurrence of sardine eggs in 1951-60 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each circle, line or dot represents a pooled statistical area (see Kramer and Smith, 1970a).

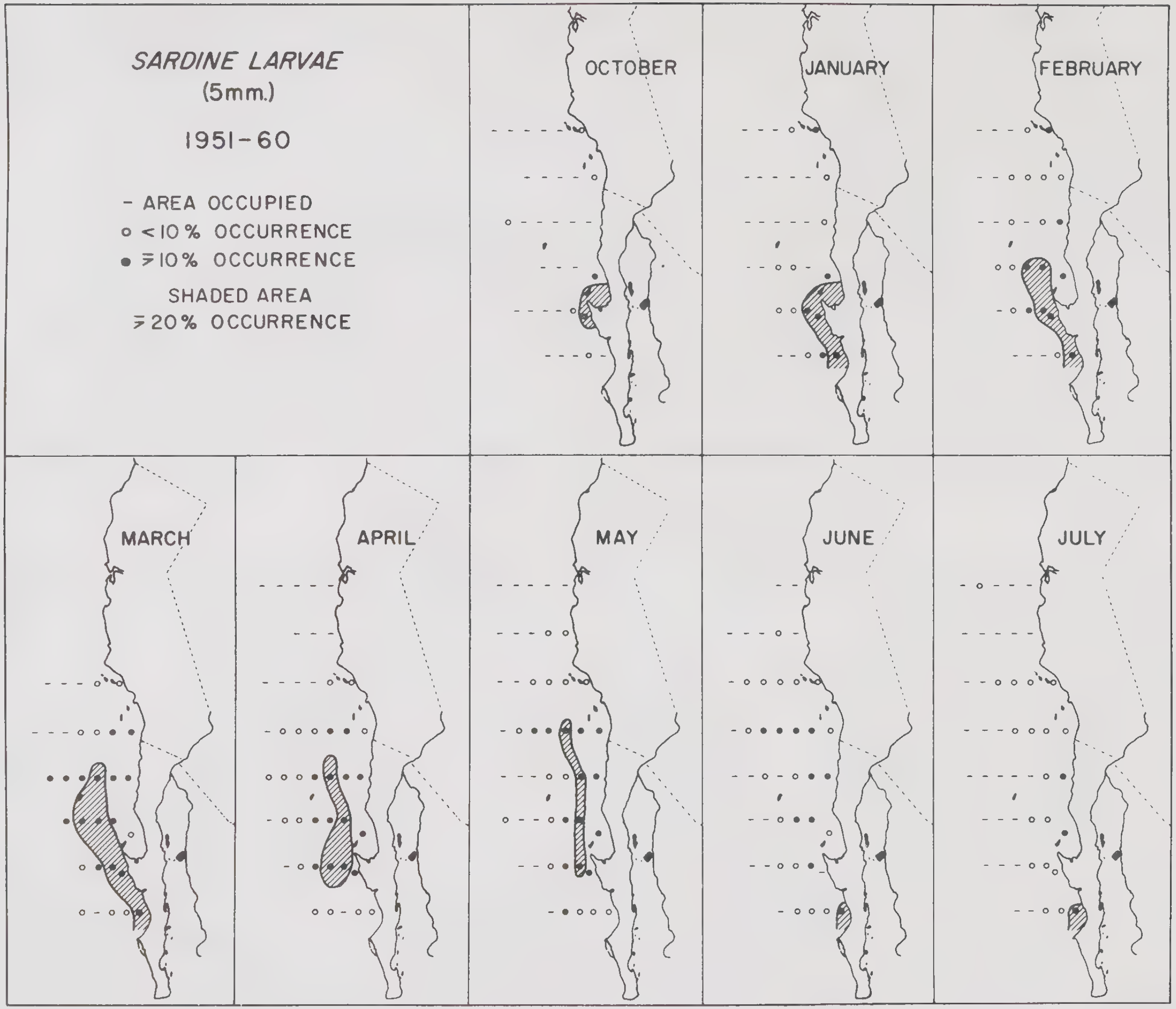
SARDINE LARVAE
(5mm.)
1951-60
- AREA OCCUPIED
○ <10% OCCURRENCE
● ⩾10% OCCURRENCE
SHADED AREA
⩾20% OCCURRENCE
OCTOBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY

Fig. 2 - Percent occurrence of 5-mm sardine larvae in 1951-60 on the survey pattern of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Each circle, line or dot represents a pooled statistical area (see Kramer and Smith, 1970a).

quantities of jack mackerel and squid. In 1968, pelagic wetfish resources (including squid) supported a catch of approximately 115 million pounds valued at over $3.1 million to the fishermen.

"A number of interrelationships exists in the wetfish fishery. Since the same basic fleet harvests different wetfish species, economic factors, changing abundance and variation in local availability, and fishing restrictions on one species may affect the fishing pressure placed upon others in the group. The northern anchovy is the sardine's principal competitor for food and occupies the same general geographic range. The increase of the anchovy population size followed closely the decline of sardine stocks. This indicates the possibility of increasing sardine stocks by increasing fishing pressures on anchovies and eliminating them on sardines. An experimental fishery to do this has been proposed, but only has been initiated on a partial basis because of political and sociological reasons."

The experimental anchovy fishery was a recommendation for 200,000 tons, discussed briefly by us (Kramer and Smith, 1971a) and detailed by Messersmith (1969).

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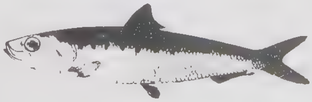

FISHERY-ADVISORY INFORMATION AVAILABLE TO TROPICAL PACIFIC TUNA FLEET VIA RADIO FACSIMILE BROADCAST

R. Michael Laurs

Fishery-advisory information is being transmitted to the tropical Pacific tuna fleet via radio facsimile (FAX) broadcast by the NMFS Fishery-Oceanography Center at La Jolla, California. Two FAX charts containing oceanographic and weather information tailored to fishermen's needs are being transmitted daily (except weekends) to vessels on the fishing grounds in the eastern tropical Pacific by NMFS-licensed radio station WWD at 2300 GMT on frequency 17294.9 kHz.

Sea-state information including swell direction and height, wind-wave height and, once each week, a 7-day sea-surface temperature analysis, is given on one chart (Fig. 1).

A second chart provides information on direction and speed of surface winds, location and direction of movement of tropical storms, location of areas of squalls and other inclement weather conditions, and location of the Intertropical Convergence Zone (Fig. 2).

Within the next month or so, a weekly analysis of thermocline depth will be included on the charts. Eventually, the location of ocean-surface temperature fronts indicated by infrared temperature measurements made by orbiting satellites and received by the Automatic Picture Transmission (APT) installation at the Fishery-Oceanography Center will be added to the charts. The geographical coverage of the charts is from the American west coast to 140° W between latitudes 30° N and 5° S.

The FAX charts are based on data received at the Fishery-Oceanography Center from many sources. These include: merchant ship marine weather and sea-surface temperature observations, which appear on Service 0 circuit 8275, the APT installation at the Fishery-Oceanography Center, Navy Fleet Numerical Weather Central at Monterey, National Weather Service storm warning bulletins and other products, and cooperating fishing vessels.

The fishery-advisory service is being performed on an experimental basis as a means of obtaining valuable environmental data from fishing vessels--and to provide fishermen with information that may assist them in making tactical fishing decisions. The environmental data collected by fishermen are necessary for use in the development of fishery-forecasting techniques and methods for tropical tunas now underway at the Fishery-Oceanography Center. The environmental data are also passed on to the Navy Fleet Numerical Weather Center in Monterey, California, and the National Weather Service for use in their programs.

The Fishery-Oceanography Center is providing FAX recording equipment to cooperating fishermen with the agreement that fishermen make and transmit ashore at least one XBT-BATHY, with probes provided by the Navy Fleet Numerical Weather Central or synoptic marine weather observation per day while on the fishing grounds. FAX equipment has been installed aboard 13 modern purse seiners during the 1971 tuna fishing season, and more installations are planned.

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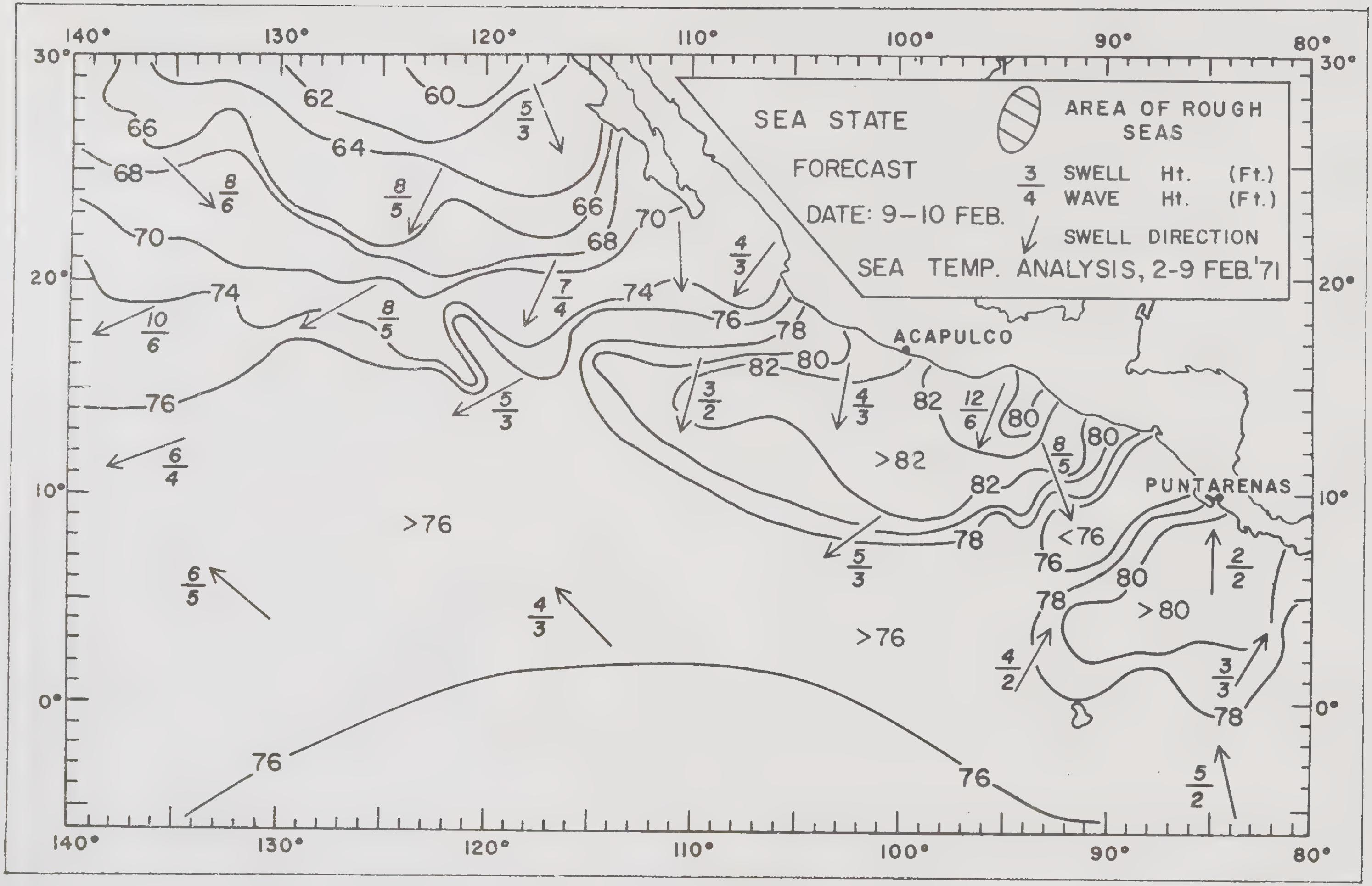
SEA STATE
FORECAST
DATE: 9–10 FEB.
SEA TEMP. ANALYSIS, 2-9 FEB.'71
AREA OF ROUGH SEAS
3/4 SWELL Ht. (Ft.)
WAVE Ht. (Ft.)
SWELL DIRECTION
ACAPULCO
PUNTARENAS
140°
130°
120°
110°
100°
90°
80°
30°
20°
10°
0°
60
62
64
66
68
70
74
76
78
80
82
>82
<76
>80
>76
5/3
8/6
8/5
7/4
4/3
10/6
6/4
6/5
3/2
12/6
2/2
3/3
4/2
5/2

Fig. 1 - Sea state forecast and sea surface temperature chart.

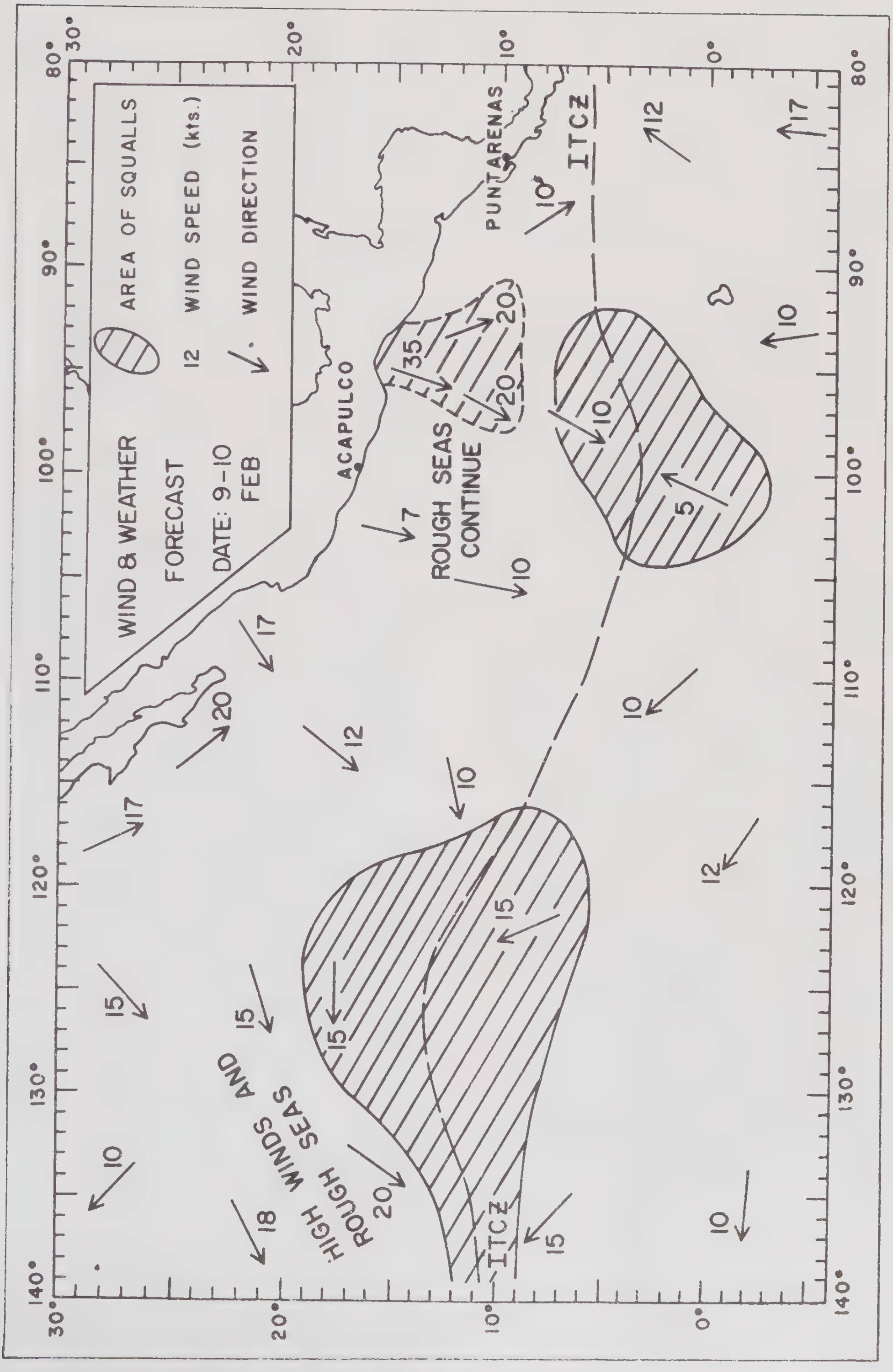
WIND & WEATHER FORECAST
DATE: 9-10 FEB
AREA OF SQUALLS
12 WIND SPEED (kts.)
WIND DIRECTION
ACAPULCO
PUNTARENAS
ITCZ
ROUGH SEAS CONTINUE
HIGH WINDS AND ROUGH SEAS
ITCZ
35
20
20
20
10
10
5
7
10
12
17
17
10
10
12
20
17
12
10
15
15
15
15
15
10
18
20
15
10
80°
90°
100°
110°
120°
130°
140°
30°
20°
10°
0°

Fig. 2 - Wind and weather forecast chart.

7124

MODELING THE RESOURCE BASE

WILLIAM H. LENARZ
National Marine Fisheries Service Fishery-Oceanography Center
La Jolla, California

I would like to start off by giving a rough idea of the magnitude of fish populations available to the San Pedro wetfish fleet. The population of northern anchovy appears to have the largest stock in the area. Estimates based on larval surveys are in the neighborhood of 2,000,000 tons. This species is followed by the jack mackerel. Admittedly crude estimates based on larval surveys place the jack mackerel population in the eastern Pacific at 2,000,000 tons. However, the San Pedro fleet harvests only relatively young jack mackerel at the southeastern edge of the population. Pacific mackerel also occur in the area. Pat Tomlinson of the California Department of Fish and Game has been studying the population dynamics of this stock. Although the stock is currently at a very low level, he has estimated that the stock could withstand a harvest of about 20,000 tons at its optimum level. The fleet has been taking about 7,500 tons of bonito per year in recent years. The bonito population has not been sufficiently studied to place an estimate on its potential. The fleet has also taken considerable amounts of bluefin tuna in the past, but this population appears to be at a depressed level and is also poorly understood. Two other commercial species occur in significant numbers in the area, the Pacific saury and squid. Attempts presently are being made to develop a fishery for saury, and hopefully we will know more about this species in the near future. About 5,000 tons of squid are landed per year. The potential appears to be much higher. Finally, I will mention the Pacific sardine. If the population ever recovers to its previous status, Murphy estimates that it will be capable of yielding about 450,000 tons per year. Perhaps half of this figure would be obtained from this area. These tonnages are impressive but meaningless until the fish are actually landed. Changes in the structure of the industry and government regulations are needed before the potential benefits from the resource can ever be obtained. Jack Baxter of the California Department of Fish and Game will present in the next talk potential landings under current conditions. I am involved in the development of a computer simulation model of the fishery to aid us in evaluating alternative methods of developing and managing the fishery.

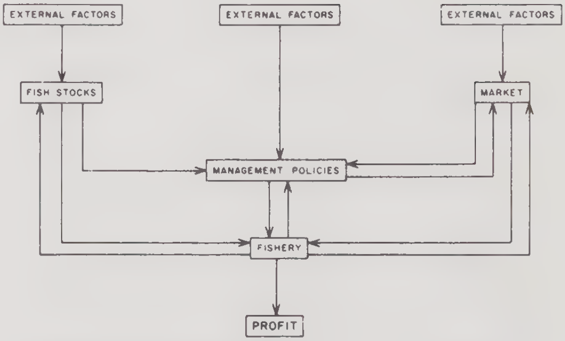

FIGURE 1. Block diagram of model of San Pedro wetfish fishery.

The first figure is a block diagram of the model. The model is composed of several sections centered about the management policies section, for the amount of profit to the fishery, the ultimate goal of any commercial enterprise, is dependent on the ability of management to estimate and interpret conditions of the fish stocks, market, and fishery. The management policies section also obtains information on external factors—for example, regulations of the northern anchovy fishery are based on strong political pressure to avoid conflicts between the commercial and sport industries. Management policies affect the fishery section and possibly to some extent the market section. The fish stocks section may be subdivided into abundance and availability sections. Abundance is defined here to be the tonnage of a population's standing stock. Availability is the portion of the population that is susceptible to the fishery. The abundance model is based on the following equation: standing stock is equal to the previous standing stock plus recruitment plus growth minus natural mortality minus yield to the fishery. Over a long period the maximum average catch for the fishery is achieved by setting each year's catch to adjust the standing stock to the level that will produce in the next season the maximum sustainable yield. The management section estimates this parameter and uses it as a factor to determine how to reach the goal of maximum profit. A simulation of availability is achieved by allowing a simulated population to migrate along shore and on and off shore. Portions of the population that are in designated areas are not available to the fishery. Again the management section uses an estimate of the availability of the population as a factor in determining how to achieve this goal. I have been talking in terms of one population, but in actuality the management policy section takes into account factors concerning several species in order to maximize profits. I plan to use linear programming techniques to do this.

"Plan" is a key word in this talk. We have developed some of the components involved but still have a ways to go before we can show any results. We are very hopeful that this symposium will provide us with ideas on how to develop the remaining components and perhaps correct any misconceptions that we have.

I would now like to present some results of a simple model of the Pacific sardine fishery that I have developed using the results of Murphy. I hope that these results will illustrate some of the information that can be obtained from the use of simulation models.

This model consists only of a fish stock section, management policies section, a simple fisheries section, and an external factors section. The fish population is simulated by a production model using Murphy's estimates of natural mortality, growth, and spawn-recruitment relationship. The model is a stochastic one in that deviations from the spawn-recruitment relationship are allowed. The occurrence of strings of successful and unsuccessful spawning years is simulated by using an auto-regressive function in generation of the deviations from the spawn-recruitment relationship. The management uses estimates of the standing stocks and recruitment to determine the amount of fishing effort needed to maintain the population at its optimum level. Errors in management's estimates of standing stock and recruitment are allowed. I used this model to study the sensitivity of yield and yield-per-effort to the accuracy of estimates of standing stock and recruitment.

Figure 2 illustrates yield as a function of accuracy. The X axis is the maximum error factor expected in 95% of the observations. For example, at the point of 3 on the X axis the maximum error in the estimate of standing stock and recruitment is within a factor of 3 of the actual value for 95% or more of the observations. The Y axis is the annual yield of sardines in tons. Four management policies were investigated. The white dots connected by the solid line in the figure represent the average annual yield from a policy of varying instantaneous rate of fishing mortality from 0 to 0.8 depending on the condition of the stock. The black dots connected by a dashed line represent the average annual yield from a policy of varying instantaneous rate of fishing mortality from 0.4 to 0.8. The explanation of the two other curves in the figure is similar. In all examples, if the estimated standing stock drops below 300,000 tons, the fishery is stopped. Each point represents a value of three simulations of 200 years. As expected, the average yield is highest when management has the most accurate information and can vary the fishing effort the most. When a management policy of using constant fishing effort at the maximum sustainable rate of 0.78 is used, the yield is 390,000 tons. This is even lower than when management uses very poor information with a varying rate of fishing mortality. Under the best management policy tried, the yield is increased about 10% over the maximum sustainable yield.

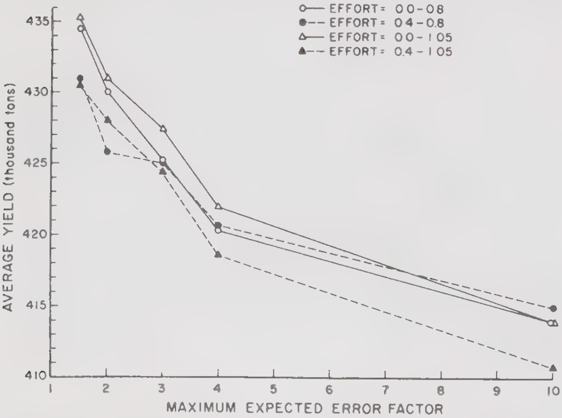

FIGURE 2. Yield of simulated Pacific sardine fishery as a function of accuracy of estimates of stock and recruitment and variability of fishery effort.

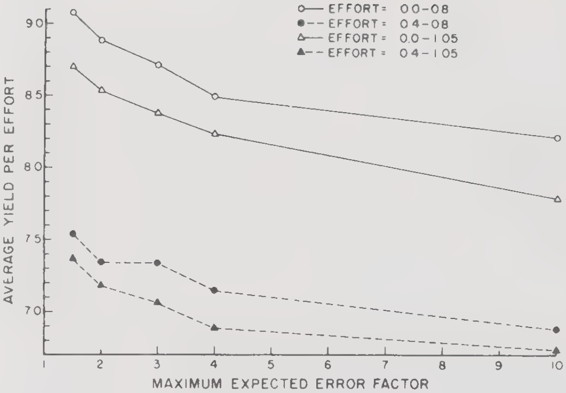

FIGURE 3. Yield per effort of simulated Pacific sardine fishery as a function of accuracy of estimates of stock and recruitment and variability of fishery effort.

Figure 3 illustrates yield per effort as a function of accuracy. This measurement is more meaningful than yield alone because it is an index of revenue per cost. Again the best results are obtained when management is well informed. The results are considerably better if the fishery is stopped when the population falls below the level of about one million tons rather than when it falls below the 300,000 ton level. The poorest result is about 40% above the result that is obtained when the population is fished at the maximum sustainable rate.

Management must take factors other than yield and yield-per-effort into consideration. One of these factors is stability of yield. Figure 4 illustrates standing stock and yield over a 200 year simulation. The maximum expected error factor was 1.5 and instantaneous rate of fishing mortality was varied between 0 and 0.8. The fishery was stopped when the spawning stock dropped below 1,000,000 tons. Even though the yield and yield-per-effort are high, very few people would be willing to accept a policy that results in such an unstable fishery. The fishery was stopped in approximately 25% of the years.

Figure 5 illustrates what happened when fishing mortality was varied from only 0.4 to 0.8 and the maximum expected error factor was 3. Yield is much more stable than in the previous case. You will note there are very few cases of when the fishery was ac-

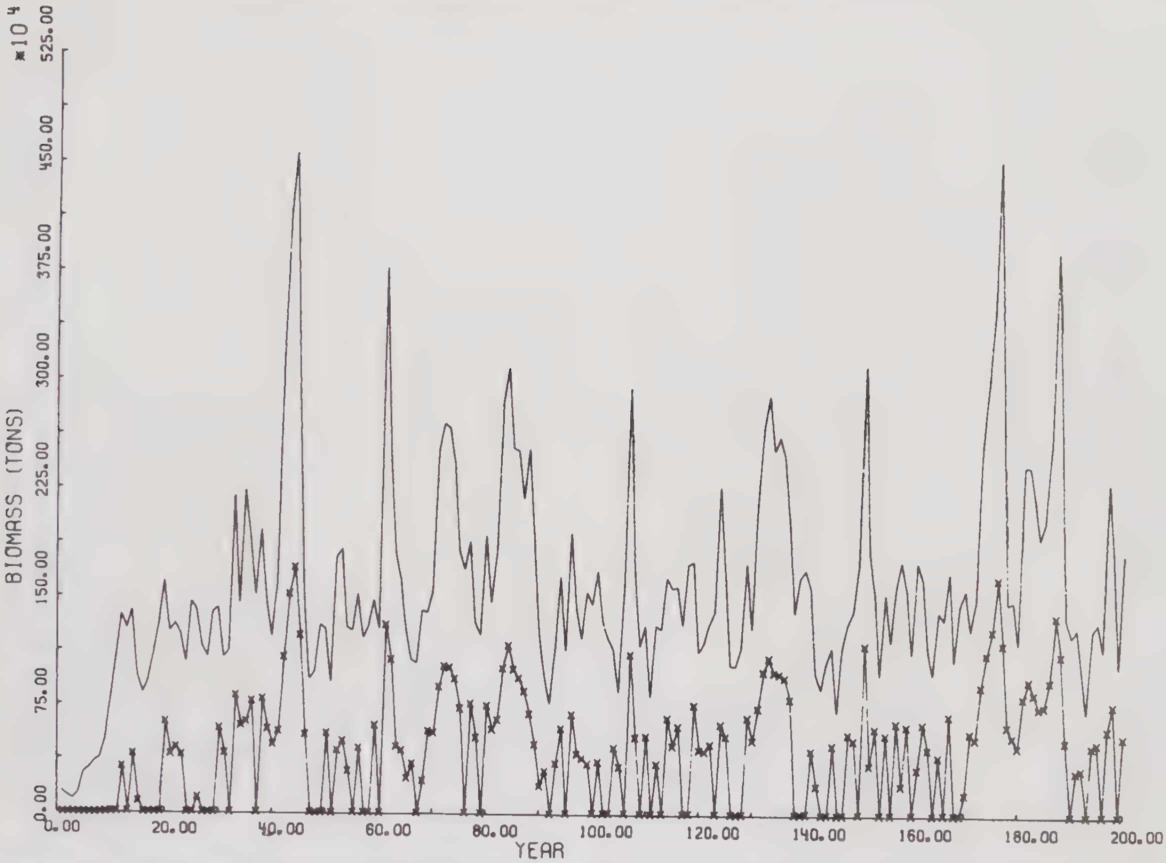

FIGURE 4. Solid line is biomass of spawning stock of simulated Pacific sardine populations. Line connecting x's is yield of simulated Pacific sardine fishery. Fishing mortality was varied between 0 and 0.8. The maximum expected error factor was 1.5. Fishing was stopped when spawning stock dropped below 1,000,000 tons.

tually stopped. In this case the fishery was only stopped when the population dropped below 300,000 tons. The average yield under this policy is only slightly less than under the previous policy.

Figure 6 illustrates the results under a policy of constant fishing at the maximum sustainable rate except when the population falls below the 300,000 tons. It is slightly more stable than the previous case. Yield is considerably less, and the yield-per-effort very much less.

Power spectra were calculated from yield under two management policies: a policy of maximum sustainable yield, and a policy of varying fishing mortality from 0.2 to 0.8. The spectra are quite similar. The power of the spectrum from the constant model is relatively slightly lower at high frequencies than that from the varied effort policy. In other words the short-term fluctuations of the yield are slightly more important in the more intensively managed fishery.

Perhaps I have stressed stable yield too strongly. As Dr. Sette has pointed out at a previous conference, we are working with a multi-species fishery. It is possible that fluctuations in profit from a properly managed multi-species fishery will be quite small. Almost all populations of fish undergo considerable fluctuations, we should strive to develop better ways of living with them.

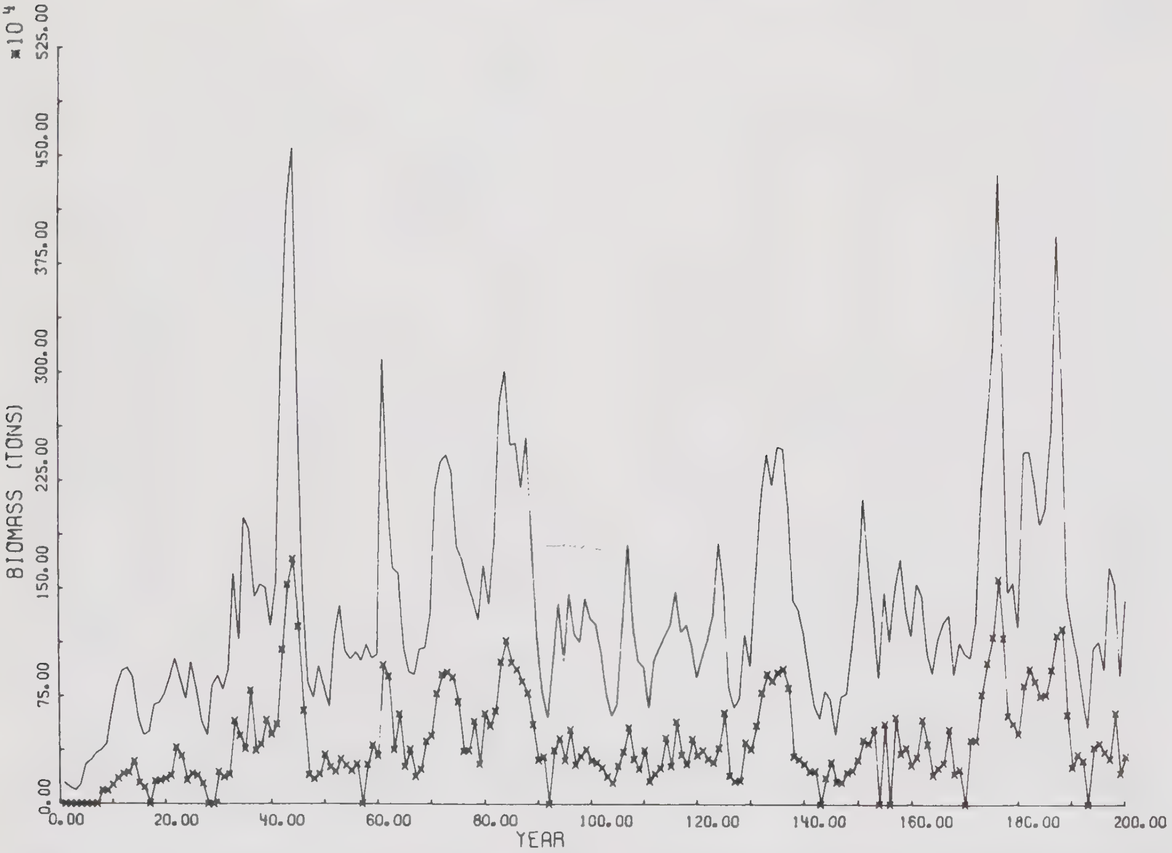

FIGURE 5. Solid line is biomass of spawning stock of simulated Pacific sardine populations. Line connecting x's is yield of simulated Pacific sardine fishery. Fishing mortality was varied from 0.4 to 0.8. The maximum expected error factor was 3. Fishing was stopped when spawning stock dropped below 300,000 tons.

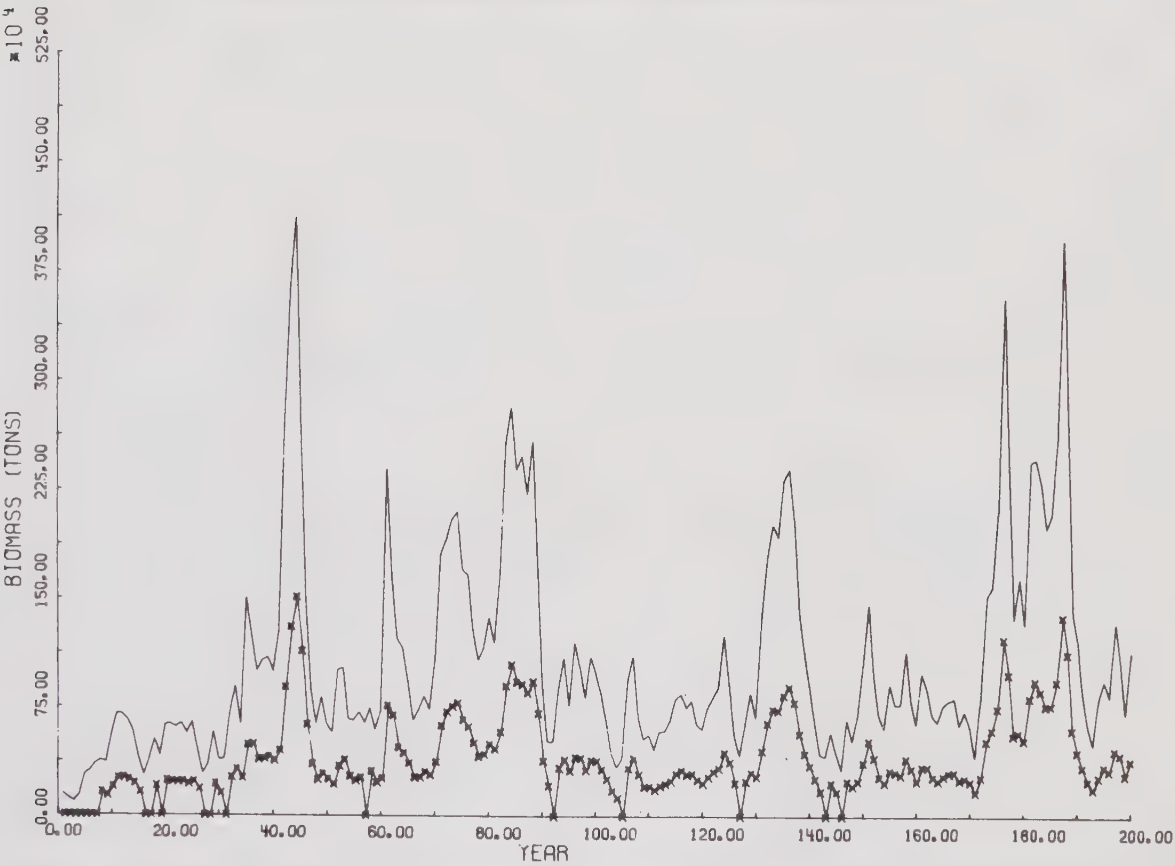

FIGURE 6. Solid line is biomass of spawning stock of simulated Pacific sardine populations. Line connecting x's is yield of simulated Pacific sardine fishery. Fishing effort was held at the maximum sustainable rate except when spawning stock dropped below 300,000 tons.

7125

Electronic Processing of Acoustical Data for Fishery Research[1]

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LENARZ, W. H., AND J. H. GREEN. 1971. Electronic processing of acoustical data for fishery research. J. Fish. Res. Bd. Canada 28: 446–447.

A system for processing acoustical data is described. Acoustical data are recorded on magnetic tape in analog form in the field. The data are converted to digital form and analyzed with the aid of a digital computer. The system provides investigators with considerably more information than is available from paper records now in common use.

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ACOUSTICAL techniques are being used increasingly for the study of fish behavior (Narver 1970; Finnell and Reed 1969) and for estimation of the size of fish stocks (Cushing 1968). Usually, acoustical returns from fish are recorded on paper charts and then counted. Counting fish targets is a subjective and tedious process and, consequently, several electronic devices have been developed to estimate target densities. An example is the echo integrator that was developed by Lahore and Lytle (1970.) These devices have been used successfully in the field (Thorne and Woodey 1970), but they are expensive and add to the complexities of field work. Another approach to estimating target densities is described in this paper: acoustical data are recorded on magnetic tape and are automatically processed by means of a digital computer.

Returning signals from a Simrad ER 4 or EK 38A echo sounder are recorded by a Sony 560 D tape recorder in analog form onto a standard four-track magnetic tape. Echo signals are recorded on one channel, and a timing pulse is recorded on the other channel as a pulse of sound is emitted by the sounder. The echo signal is recorded as a 6-kHz sine wave, 100% amplitude modulated by the returning echo from the sounder. The operator of the sounder records a vocal log at the beginning of each set of soundings onto the tape.

The data are converted from analog to digital form by a unique analog-to-digital converter that the Department of Atmospheric Sciences of the University of Washington constructed. We developed electronic circuitry to reduce the data to a more efficient form during the digitizing process.

Figure 1 illustrates the nature of the signal from the time that it is emitted by the sounder until it has been converted to digital form. The signal from the tape recorder is passed through a full-wave rectifier. This device can be expressed mathematically by the equation

$$V_{\text{out}} = |V_{\text{in}}|, \qquad (1)$$

where V_{out} = output voltage, and V_{in} = input voltage. Then the timing pulse is subtracted from the signal so that all information is stored in one series of data. It is simple to distinguish the negative timing pulse from the remainder of the data. Next, the signal is passed through a 1-kHz, low-pass filter. We choose a 1-kHz cut-off frequency because the length of the pulse of sound transmitted by the sounder is about 1 mv-sec, thus there should be no significant variations at frequencies higher than 1 kHz left in the return signal.

Much of the signal contains data that are not interesting to us. We are never interested in echos returning from depths greater than 100 m. In many instances, only the upper 30–40 m are of interest. We developed a timing gate to eliminate the unnecessary data. This device allows us to reduce the amount of data by more than 80%. Since returns from adjacent pulses of sound are highly correlated, it is not always necessary to sample every pulse to obtain desired results. Therefore, we developed a device to allow us to sample every first, second, third, or fourth pulse. The data are digitized then at a 2-kHz rate and recorded in binary form on magnetic tape.

A computer program was written in the Fortran language for a Control Data Corporation 6400 computer to perform preliminary analyses of the data. Since an enormous amount of data is involved (an average of 18,000 observations per minute

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of sounding), particular attention was devoted toward developing an efficient program. The data are packed five observations per 60-bit computer word. Most of the calculations are made in integer mode.

Several calculations are made by this program. During the digitizing process, a record of data is created without movement of the analog tape. This group of data represents the noise level of the system. The average noise level is calculated and subtracted from each observation. Changes in gain of the digitizing system are estimated from the timing pulse. The gain is standardized by multiplication of each observation by a standard value divided by the minimum value of the timing pulse within a specified time interval. The user is allowed to supply a TVG (time varying gain) function, which corrects for increased attenuation of the signal with depth. Voltage and voltage squared are summed at user-specified intervals of time and depth. Statistical frequency distributions of target strengths are produced at specified intervals of time, target strength, and depth.

The calculations made by this program represent a minimal analysis of the data. We anticipate that the availability of acoustical returns from fish targets in digital form will facilitate the development of methods of target classification. Figure 2 is a three-dimensional plot of returns from a target in Iliamna Lake, Alaska. There is considerably more information available to investigators than would be available from paper recordings now in common use.

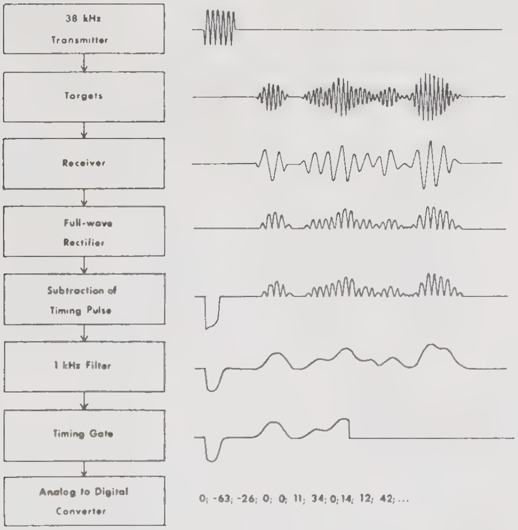

FIG. 1. Flow chart of acoustic signal from emission by sounder to conversion to digital form.

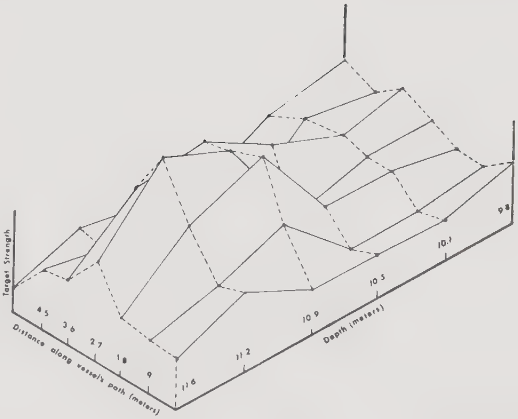

FIG. 2. Three-dimensional plot of echo returns from a target in Iliamna Lake, Alaska.

A detailed description of the electronic circuitry and computer software may be obtained from the Fisheries Data Analysis Center, Fisheries Research Institute, Univeristy of Washington, Seattle, Wash. 98105, USA.

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7126

INDUCED SPAWNING OF THE NORTHERN ANCHOVY, *Engraulis mordax* GIRARD

Roderick Leong[1]

ABSTRACT

Anchovies were induced to mature their gonads by an artificial photoperiod of 4 hr light and 20 hr darkness at 15° C. Single injections of suspensions of salmon pituitary, carp pituitary, or a solution of human chorionic gonadotropin (HCG) promoted increase in egg diameters but did not induce spawning. Two injections, a first of HCG and the second 2 days later of either salmon pituitary or carp pituitary, induced spawning. At each spawning 6,000 to 16,000 eggs were collected, and 25% to 80% of the eggs hatched. Larvae grown from these eggs were morphologically similar to those caught in the sea.

An investigation was started at the National Marine Fisheries Service Fishery-Oceanography Center, La Jolla, Calif., in 1969, to examine methods for spawning the northern anchovy, *Engraulis mordax* Girard, under controlled laboratory conditions in order to supply eggs and larvae for experimental studies. The strategy for spawning anchovies in captivity was to provide an environment in which the fish would mature their gonads and subsequently to induce spawning through hormone treatment. The role of the environment and the use of hormone injections for inducing spawning in other species of fish has been well documented by Pickford and Atz (1957). This report describes a method for bringing the anchovy to ripeness and the effectiveness of various hormone treatments in inducing spawning. As far as is known this was the first successful attempt to artificially mature and spawn this pelagic fish in the laboratory

MATERIALS AND METHODS

Anchovies, averaging 90 mm in length, were purchased from a San Diego bait dealer in March of 1969, transported to the laboratory, and held in circular plastic lined wading pools 4.6 m in diameter with 0.9 m of water. By the beginning of the injection trials in August of 1970, the fish had grown to an average length of 125 mm, at which length half of the fish should have been mature (Clark and Phillips, 1952). The fish were subjected to a photoperiod of 4 hr light (32 ft-c at the brightest spot on the surface of the water) and 20 hr dark (1 ft-c) for 3 months prior to the trials. Observations in the preceding year revealed that anchovies tend to mature more readily under relatively prolonged dark conditions. The tanks were constantly supplied with fresh seawater and the temperature was maintained at 15° C (Lasker and Vlymen, 1969). Much of the spawning of anchovies in nature occurs at or near this temperature (Ahlstrom, 1956). The fish were fed twice a day. In the first feeding, given at the beginning of the 4-hr light period, the fish were fed 6% of their live body weight in rotating daily rations of ground squid, ground anchovies, and brine shrimp. In the second feeding, given near the end of the light period, the fish were fed 1% of their body weight in trout chow.[2] Under this light, temperature, and food regimen approximately one-fourth of the fish developed gonads which weighed more than 6% of their body weight.

Three series of injection trials were conducted. In the first series the following dosages and types of injections were tested: 2.5, 5.0, and pituitary[3] prepared essentially by the method of 10.0 mg of salmon (*Oncorhynchus tshawytscha*)

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[1] National Marine Fisheries Service Fishery-Oceanography Center, La Jolla, Calif. 92037.

[2] Ralston Purina trout chow, size 2. Reference to commercial products does not imply endorsement.

[3] Obtained through the courtesy of Dr. Irwin Haydock and the California Department of Fish and Game, Nimbus Fish Hatchery, Rancho Cordova, Calif.

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Haydock (1971), 2.5, 5.0, and 10.0 mg of commercial carp pituitary,[4] 1.0, 2.5, and 5.0 mg of deoxycorticosterone acetate (DOCA),[5] 1.0 mg of luteinizing hormone (PLH),[6] and 25, 50, and 100 international units (IU) of human chorionic gonadotropin (HCG).[5] The treatments were given in single 0.1-ml injections using a carrier of Holtfreter's solution (Emmel and Cowdry, 1964) in all cases except for DOCA where sesame oil was used. The suspensions of pituitary were prepared by triturating a weighed quantity in a small tissue grinder with enough liquid to form the proper concentration. The suspension was then pipetted into a small serum bottle where it could be withdrawn with an injection syringe. The injections were administered intraperitoneally with a 24-gauge needle between the pelvic fin and vent. Prior to injection the fish were anesthetized in 50 liters of water with 7 ppm quinaldine (Vrooman and Paloma, 1966).

Under each treatment 12 to 15 fish were injected. The sex and level of ripeness of living anchovies are difficult to distinguish and a portion of the fish in these trials were immature. Therefore it was necessary to inject this relatively large number of fish to increase the probability that some would be sufficiently developed to respond to hormone injections. Injected fish were placed in small holding tanks 1.2 × 1.2 m with 0.9 m of water. These tanks had running seawater and the temperature was also maintained at 15° C. Nets with 202-μ mesh were placed at the outflows of these tanks to collect eggs in the event of spawning. If no spawning occurred after 48 hr, the fish were stripped and fertilization attempted by the dry method (Davis, 1961). In this method the eggs and sperm are expressed, mixed, and left to stand in a dry container for 5 to 10 min before being placed in water. It was noticed in all trials that at least some males produced motile sperm.

The fish were killed after stripping and ovaries were removed from the females. Each ovary was teased apart and the major diameters of the most advanced eggs measured. The maximum diameters of injected fish were compared with the diameters of more than 500 captive uninjected females sampled during the previous 16 months to determine which of the treatments were effective in producing growth.

The effect of two injections of different hormones were examined in the second series of trials. The first injection was 50 IU of HCG and the second, given 48 hr later, was one of the following: 2.5 mg of salmon pituitary, 10.0 mg of carp pituitary, 5.0 mg of DOCA, 1.0 mg of PLH and 250 IU of gonadotropin from pregnant mare serum (PMS).[6] The methods of anesthetizing, injecting, and holding of fish were the same. If spawning did not occur within 48 hr after the second injection, the fish were stripped and fertilization attempted. In this and the final series of trials the fish were not killed after stripping and measurements of egg diameters were not made. Here the only criterion for success was spawning or production of viable eggs through stripping.

The effect of three injections of the same hormone was tested in the third and final series of trials. One group of fish was given three injections of 2.5 mg of salmon pituitary and another group three injections of 50 IU of HCG. The injections were spaced a day apart and the procedures were the same as described earlier. If no spawning occurred within 24 hr after the third injection, the fish were stripped and fertilization attempted.

RESULTS

None of the fish that were given a single injection spawned or produced viable eggs through stripping. Most of the stripped eggs were clumped, opaque, and apparently had not ovulated. Some of the treatment, however, produced noticeable increases in egg diameters. Table 1 shows the number of females under the various single-injection treatments and the number with and without eggs larger than 1.0 mm. The number of females was small in some

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[4] Purchased from Stoller Fisheries, Spirit Lake, Iowa.

[5] DOCA and HCG purchased from Sigma Chemical Co., St. Louis, Mo.

[6] PLH and PMS purchased from Calbiochem, Los Angeles, Calif.

TABLE 1.—Female anchovies after various hormone injections having eggs larger than 1.0 mm in diameter. The occurrence of females with eggs larger than 1.0 mm is considered to be an indication of induced egg maturation. Of more than 500 captive uninjected fish sampled during the previous 16 months none had eggs larger than 1.0 mm. The average injected fish weighed about 25.0 g and measured 125 mm in length.

Type of injection	Dose/fish	No. females injected	No. females with eggs >1.0 mm
Salmon pituitary (*Oncorhynchus tshawytscha)*	2.5 mg	8	2
	5.0 mg	7	4
	10.0 mg	8	1
Commercial carp pituitary	2.5 mg	5	0
	5.0 mg	3	0
	10.0 mg	4	1
Human chorionic gonadotropin (HCG)	25 IU	4	1
	50 IU	8	1
	100 IU	6	0
Deoxycorticosterone acetate (DOCA)	1.0 mg	3	0
	2.5 mg	6	0
	5.0 mg	8	0
Luteinizing hormone (PLH)	1.0 mg	4	0

cases because most of the injected fish were males or had died through handling. Of the more than 500 females examined during the previous 16 months, none had eggs larger than 1.0 mm. The occurrence of females, Table 1, with eggs larger than 1.0 mm indicates that salmon pituitary, carp pituitary, and HCG are capable of promoting overnight growth of eggs. Salmon pituitary appeared to be the most potent for producing growth. The largest eggs observed were over 1.3 mm in diameter and within the size range, 1.23 to 1.5 mm, of naturally spawned eggs (Bolin, 1936). DOCA and PLH at the dosages tested were not effective in stimulating egg growth. The preponderance of fish with smaller eggs may be due to a low state of ovarian development at the time of injection.

In the second series of trials, HCG followed by DOCA, PLH, or PMS did not induce spawning and subsequent stripping produced only unovulated eggs which were not successfully fertilized. The combinations of HCG followed by salmon pituitary and HCG followed by carp pituitary induced spawning within 18 hr after the second injection. The fish spawned and fertilized the eggs themselves and large numbers of eggs were caught in the nets at the outflows of the tanks. Spawning was repeated several times with each of these two combinations of injections. The spawnings produced from 6,000 to 16,000 eggs with the percentage hatching varying from 25 to 80%. The larvae from these induced spawnings appeared morphologically normal and many were reared past 25 days by the methods of Lasker et al. (1970). The differences in the hatching percentage may be attributed to variation in the state of gonad development of parent fish at the time of injections.

The number of eggs collected suggests that only one or two females from any of the spawning groups contributed eggs. According to estimates by MacGregor (1968) female anchovies spawn almost 600 eggs per gram of fish. The average female in these trials weighed approximately 25 g and should have produced nearly 15,000 eggs. Only one or two females from any of the twice-injected groups extruded ovulated eggs upon stripping. Although the eggs were translucent and measured about 1.5 mm in diameter less than 10% hatched after being mixed with motile sperm.

In the final series of trials, three injections of salmon pituitary or three injections of HCG over a 3-day period failed to induce spawning. The stripped eggs were opaque and fertilization was not successful. These limited results suggest that the combination of HCG followed by salmon pituitary is more effective for induction of spawning than when these hormones are administered alone.

The results of these injection trials demonstrate that the northern anchovy can be induced to spawn in captivity and two effective treatments are HCG followed by salmon pituitary or HCG followed by carp pituitary after gonads are matured by a specific light-dark treatment of the fish. The induction of spawning of anchovies in the laboratory provides a practical way for supplying viable eggs for studies on larvae. In this study the time of spawning was controlled and eggs can probably be produced the year around if a large stock of fish is maintained. This was emphasized by the fact that the fish in this study were induced to spawn during the late summer and fall months when anchovy eggs are virtually absent from the sea off San Diego. As far as is known, these are the first reported spawnings of *Engraulis mordax* in captivity and the first hormone-induced spawnings of engraulids.

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7127

LABORATORY STUDIES OF PREDATION BY MARINE COPEPODS ON FISH LARVAE

KURT LILLELUND[1, 2] AND REUBEN LASKER[3]

ABSTRACT

A variety of marine copepods have been shown to fatally injure or capture and ingest young anchovy larvae in the laboratory. *Labidocera jollae, L. trispinosa,* and *Pontellopsis occidentalis* (family Pontellidae), species common to surface waters of the California Current, are effective predators of larval fish. The copepods can be attracted by the vibrations of the larval tail beat and react by biting or capturing the fish larvae. Cruising speeds for these copepods varies from 1.5 to 4 body lengths per second which, coupled with continuous swimming behavior, results in extensive searching by the copepod for prey. In laboratory experiments, when the ratio of larval fish prey to *L. jollae* female individuals was low (<10:1 in 3500 ml), all of the larvae were killed in 24 hr where "killing" refers to both capture-ingestion and biting resulting in a fatality. If the ratio was higher, killing increased but rarely reached 100% mortality of the larvae. *L. trispinosa* males and females never killed all the larvae offered to them in 24 hr in 3500 ml although more larvae were killed as the number offered was increased. Increased swimming and escape ability developed as anchovy larvae became older and were not caught or bitten as effectively as younger ones by copepods. However, killing of larvae by *P. occidentalis* was unaffected by the age of the larvae up to 3.5 days old.

When *Artemia salina* nauplii were substituted for larval fish as prey for *L. trispinosa*, the amount of grazing was proportional to the ratio of nauplii to copepods. If the number of *Artemia* nauplii was less than 11-14/liter per copepod in 3500 ml all the nauplii were killed in 24 hr. When the density of nauplii was increased, more were killed but never all of them. In experiments where nauplii and yolk-sac larvae were offered together as prey the mortality of the larvae due to predation declined in proportion to the increase in the number of nauplii provided.

Caloric requirements were calculated from oxygen consumption measurements and showed that only 1 to 4 anchovy larvae are required per day per copepod to satisfy the metabolic needs of *Labidocera,* depending on the species and the sex. This number is far less than can be killed or captured if the density of larvae is high enough.

In large (140 cm) vertical cylinders larvae and *L. trispinosa* were distributed within 25 cm of the surface in the dark. Data are presented which show that *L. trispinosa* and anchovy larvae also co-occur in the upper few meters under the surface of the sea. This is probably also true for *P. occidentalis* and *L. jollae.* No data are yet available on the relative density of predatory copepods and fish larvae where they co-occur or their possible predator-prey interactions in the sea.

Huge mortalities of larval fish are known to occur in the sea. From the time of Hjort (1914) these have been attributed mainly to the lack of the proper food when the larvae begin to feed (see review by Blaxter, 1969). Undoubtedly other biotic and abiotic factors are also involved in larval fish mortality, but comparatively little work has been done to measure their effect. Among the possible causes of larval-fish mortality, predation by other zooplankters may be an important factor. Freshwater aquarists have known for some time that copepods must be eliminated from fish rearing tanks or high mortalities of young larvae or fry will occur (Davis, 1959). Lillelund (1967) reviewed the literature pertaining to predation by freshwater copepods on fish larvae and described the predatory behavior of cyclopoid copepods as he observed them

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in the laboratory. Zooplankters in general and copepods in particular have been seen to devour marine fish larvae. For example, in an early study on the rearing of marine fish, Garstang (1900) noted that the harpacticoid copepod *Idya furcata* (= *Tisbe furcata*) was a larval-fish predator. Subsequently Lebour (1925) from her examination of living marine plankton, concluded that a variety of zooplankters eat fish larvae and noted that "many jellyfishes and *Pleurobrachia* besides *Sagitta* and *Tomopteris* will readily eat small fishes." Lebour also illustrated the capture of an anglerfish larva (*Lophius piscatorius*) by the copepod *Anomalocera pattersoni* (family Pontellidae).

Despite this information on the predatory behavior of copepods, there is virtually no behavioral information available on the ability of marine copepods to capture and ingest or fatally injure fish larvae, although many marine copepods are known to be carnivorous (Gauld, 1966) and other incidental reports of copepods predatory on marine fish larvae have been made (Wickstead, 1965; Petipa, 1965). Furthermore, the possible importance of predation on fish larvae as it affects the determination of year class strength through larval fish mortality has been generally ignored, probably because of the lack of pertinent quantitative laboratory and field information.

In this study we present the results of experiments designed to measure quantitatively the ability of three pontellid marine copepods, *Labidocera trispinosa, L. jollae,* and *Pontellopsis occidentalis,* to capture or fatally injure larvae of the northern anchovy, *Engraulis mordax,* an important commercial fish of the California Current. The behavior of copepods and larvae which bears on the susceptibility of the latter to predation is also described in detail.

METHODS

Copepods and anchovy eggs were captured with a 0.5-m-mouth-diameter plankton net (0.333-mm mesh) towed at the surface in coastal water off San Diego, Calif., between March and August 1970. The copepods were separated from other plankton with a large bore pipette on shipboard, diluted with surface water in liter jars, and kept at sea water temperature (about 15° C) in an insulated chest until returned to the laboratory.

All experiments were performed in 3500-ml beakers in the dark because *Labidocera* were phototactic and attracted to the light source and *Pontellopsis* was inhibited in its attacks on larvae in the light. In an earlier study on freshwater cyclopoid copepods, Lillelund (1967) used a constant level, continuous flow device which we used also for maintaining marine copepods in good condition in the laboratory (Figure 1). However, it was more convenient to do all predation experiments in static water over a 20- to 24-hr period, since the copepods we investigated swim continuously throughout the small volume (3500 ml), obviating the need for continuously circulated water. A constant temperature of 18° C was maintained in the beakers by placing them in a running seawater bath.

Mortality of the larvae was measured by taking the difference between the number of larvae at the beginning of the experiment and those remaining alive at the end. Some mortality not associated with predation always occurred, hence control vessels containing larvae alone were always provided and the results of experiments corrected for larvae dead of other causes. In all experiments, this natural mortality never exceeded 10%.

Anchovy eggs were sorted in the laboratory according to their stage of development and newly hatched larvae were used as prey in the predation experiments. When older larvae were required they were reared according to the method of Lasker et al. (1970), except that the rotifer *Brachionus plicatilis* was substituted for snail veligers as larval-fish food (Theilacker and McMaster, in press).

Oxygen consumption measurements were made by Warburg manometry. Usually 18 to 22 copepods were put into 3 ml of seawater in a Warburg flask and oxygen uptake monitored for 8 hr at 18° C. Dry weight of individual copepods was measured with an electrobalance to ± 2 μg.

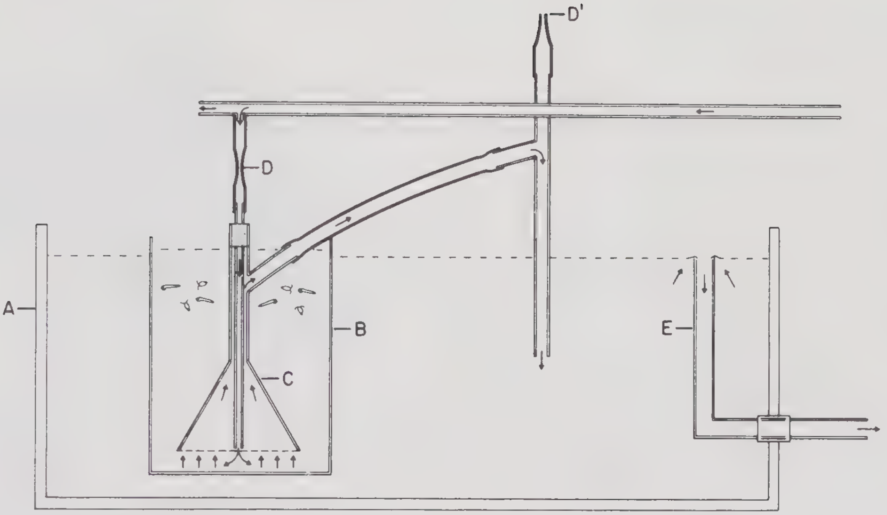

FIGURE 1.—Constant level device for maintaining copepods and fish larvae. The temperature of the 3500-ml beaker (B) was kept constant with running seawater in a water table (A) whose capacity was 610 liters. Plankton netting (0.333-mm mesh) was held over the mouth of the 500-ml funnel (C) with a section of bicycle tire tube. Rubber tubing showing constrictions as D and D′ had screw-type clamps to regulate flow. E is the drain. Note that the level of seawater is higher in the beaker than in the bath. The drawing is not to scale.

MARINE COPEPODS CAPABLE OF KILLING ANCHOVY LARVAE

Before choosing *Labidocera* and *Pontellopsis* for experimental work we tested a number of copepod species for their ability to capture or fatally injure newly hatched yolk-sac larvae of the northern anchovy. For each test, five fish larvae were isolated in 200 ml of seawater in a Petri dish at room temperature (20° C) usually with two or three copepods of a particular species to be tested. Of the local copepod species observed, the following fatally injured anchovy larvae by biting them or captured and ingested them:

Acartia dana and *A. tonsa*
Euchirella rostrata and *E.* sp.
Labidocera jollae and *L. trispinosa*
Pleuromamma borealis
Pontellopsis occidentalis
Euchaeta acuta
Euaetideus acutus
Candacia bipinnata

Because the two species of *Labidocera* listed above are common to waters adjacent to San Diego and were readily available, most of our experimental work was done with them. When *Pontellopsis occidentalis* became abundant, we also collected some information about its predatory behavior relative to fish larvae.

Although capture and ingestion of fish larvae was commonplace under laboratory conditions, it is rare to find a copepod with a captured fish larva in Formalin-preserved plankton. This may be the result of the Formalin preservation common on shipboard which, we have observed, usually causes copepods to drop larvae.[4]

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[4] We have found that if a copepod has captured a larva it will retain the larva if both are transferred together to a slight melted depression in an ice cube with a pipette and preserved with a drop of 3% Formalin.

SWIMMING AND FEEDING BEHAVIOR OF *Labidocera*

REACTION TO THE LARVAL TAIL BEAT; BITING AND INGESTION OF LARVAE

We noted that individual *Labidocera* ignored motionless fish larvae or floating eggs. However, when a larva beat its tail in the close vicinity of a swimming labidoceran, the copepod swam immediately toward the beating tail and grasped the larva. The tail beat of the larva was often stimulated by the chance touch of a copepod's antenna. Figures 2a and 2b show a *L. jollae* female which caught a 3-day-old anchovy by the tail and partially ingested it. Figure 3 shows another larva caught behind the head by another female. Response to the larval tail beat is typical of all the copepods we have observed which attack fish larvae.

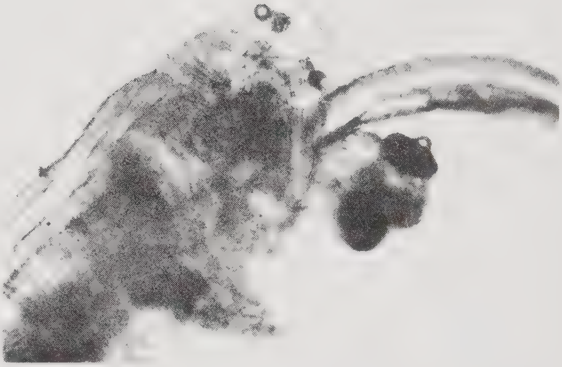

FIGURE 3.—The head of a *Labidocera jollae* female showing a newly captured 3-day-old anchovy larva caught behind the head.

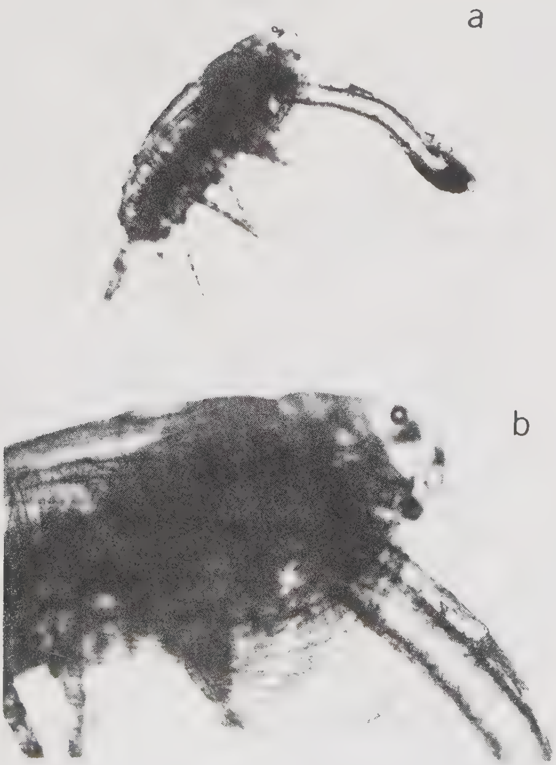

FIGURE 2.—(a) *Labidocera jollae* female, 3 mm long, and a 3-day-old anchovy larva 6 mm long which was captured by the tail and half ingested. (b) Enlargement of the head and setae of the copepod shown in 2a.

Often a copepod would capture, then drop a larva, inflicting a wound by biting the thin epithelium. The anchovy larval skin is only about 2 to 3 μ thick in the finfold and tail regions and appears to be easily injured. In every instance, a bite which damaged the larval skin resulted in the death of the larva. Therefore, in our experiments mortality due to a copepod was the result of either actual capture and ingestion of a larva or biting that resulted in damage fatal to the larva. Hence, the number of larvae reported as "killed" in an experiment is the sum of fatalities due to biting and the number of larvae actually ingested. For both sexes of each *Labidocera* species the time of ingestion of anchovy larvae varied between 6 and 25 min. In one instance an *L. trispinosa* male caught and completely consumed two larvae in 1 hr. If we increased the number of larvae to six or more in a 200-ml Petri dish containing two copepods, mortality through biting alone increased and the time during which a larva was held by a copepod varied from a few seconds to minutes. For example, an *L. jollae* female attacked six larvae in 50 min. The individual larvae were held only 10 to 60 sec and not ingested. All six larvae died subsequent to the attack.

POSITIVE PHOTOTAXIS AND SWIMMING SPEED

Labidocera jollae and *L. trispinosa* are positively phototactic, and when confined to a beaker of seawater illuminated from above, concentrate at the water surface-beaker interface which is the brightest area. Copepods were induced to swim in the main body of water by wrapping the beaker with black paper with 1 cm lapped around the rim. This effectively eliminated the bright area and resulted in random swimming movements of the copepods near the surface.

Swimming distances of copepods were traced for 3 min in two dimensions on a clear acetate sheet laid over a glass plate on top of a 3.5-liter beaker. The distances were measured with a map measurer. Vertical movements were very slight, thus negligible, in these experiments because of the highly phototactic behavior of the individuals. Labidocerans can swim continually over relatively large areas in short periods of time (Vlymen, 1970). Comparative speeds for individuals are shown in Figure 4; on the average a *L. jollae* female swims 62 cm/min (3-4 body lengths/sec) and the male swims 22 cm/min (1.5-2 body lengths/sec). Both sexes of *L. trispinosa* swim 33 to 37 cm/min (2-3 body lengths/sec). Although *L. jollae* females swim in a seemingly random pattern, the males usually swim in straight lines for a few seconds then swim in circles and cover a small area intensively.

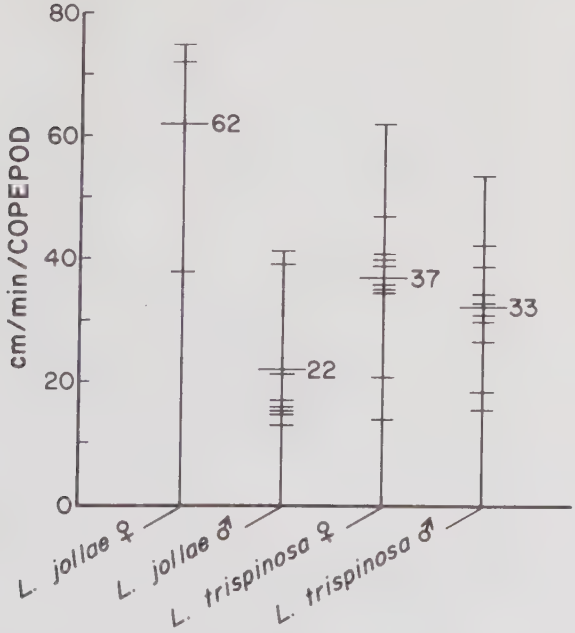

FIGURE 4.—Swimming speeds for individuals of *Labidocera*. Each small horizontal bar represents the speed of one animal; the large bar is the mean speed.

KILLING EFFICIENCY OF *Labidocera*

We discovered that if the ratio of anchovy larvae to *L. jollae* females was low (<10:1), all or almost all the larvae in 3500 ml would be killed within 20 to 24 hr in the dark. Two experiments were done which illustrate this. In the first, 30 anchovy larvae were confined with a variable number of *L. jollae* females (Figure 5) resulting in concentrations of larvae to copepods

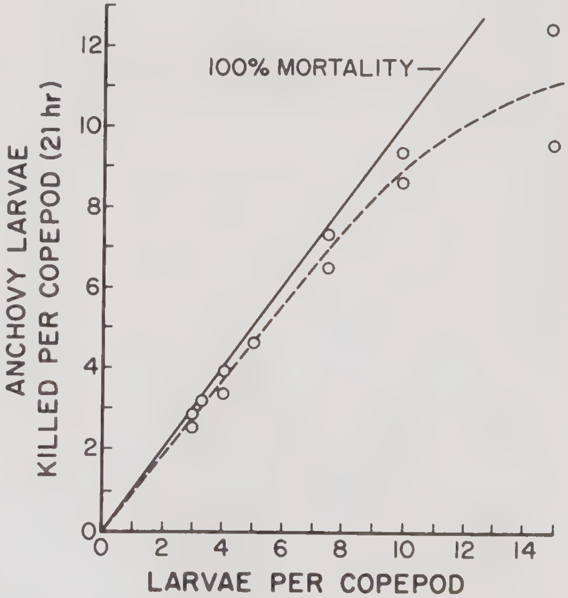

FIGURE 5.—Mortality of *Engraulis mordax* larvae, 0 to 1 day old, resulting from predation by different numbers of *Labidocera jollae* females. In each experiment 30 larvae were presented to 2 or more copepods in 3500 ml for 21 hr. Thus where 3 larvae per copepod is indicated on the abscissa, 30 larvae and 10 copepods were used; at the other extreme 15 larvae per copepod indicates 30 larvae and 2 copepods. The unbroken line is the theoretical 100% larval mortality curve.

of 3:1 to 15:1. In the other, only single *L. jollae* females were tested and the number of larvae varied to provide ratios of larvae to copepods of 5:1 to 40:1 (Figure 6). The results were similar in the two experiments; when the ratio was approximately 10:1 or less, it was usual for all larvae to be killed. When more than 10 larvae were available per copepod, more larvae were killed per copepod but the mortality dropped below 100%. In similar experiments two *L. trispinosa* females were tested with larvae to copepod ratios varying from 2:1 to 15:1. *L. trispinosa* females were much less efficient than *L. jollae* females and never killed all the larvae presented to them in 24 hr (Figure 7). Males of both species were similar in killing efficiency to *L. trispinosa* females. Based on these results, further predation experiments were performed over 20 to 24 hr using 30 larvae with two *L. jollae* females or five males; experiments performed with either sex of *L. trispinosa* had 30 larvae and 5 copepods. The comparative predatory ability of labidocerans is shown graphically in Figure 8. The mean number of anchovy larvae killed by *L. jollae* females was 15. *L. trispinosa* males and females had mean kills of 4 and 2 larvae respectively in 24 hr, markedly less than *L. jollae* females. The high killing rate by *L. jollae* females reflects the longer distances and greater volume covered by them owing to their larger size. *L. jollae* females are approximately 0.2 mg dry weight, and males, 0.1 mg. Female *L. trispinosa* average about 0.1 mg dry weight; males, 0.09 mg.

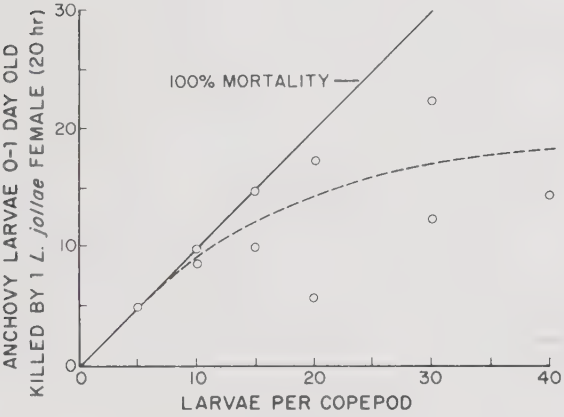

FIGURE 6.—Mortality of *Engraulis mordax* larvae, 0 to 1 day old, resulting from predation by single *Labidocera jollae* females. In each experiment 1 copepod was confined with 5 to 40 larvae in 3500 ml for 20 hr. The unbroken line is the theoretical 100% larval mortality curve.

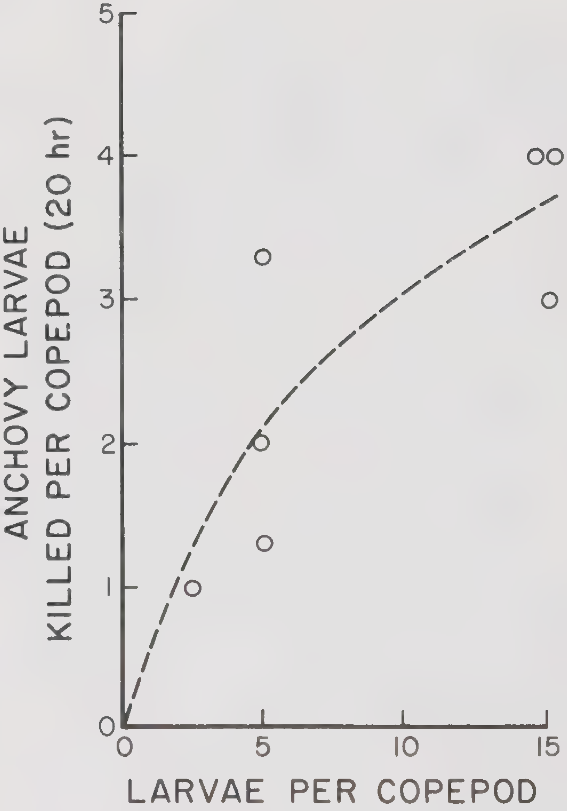

FIGURE 7.—The effect of increasing the density of larval anchovies on the predatory behavior of *Labidocera trispinosa* females. Each dot represents a separate experiment with 2 or 3 copepods and from 5 to 45 larvae.

EFFECT OF THE AGE OF THE LARVA ON PREDATION BY *Labidocera*

We noted in our experiments that *Labidocera* became less efficient in killing anchovy larvae as the larvae aged. The anchovy larva is 2.5 mm

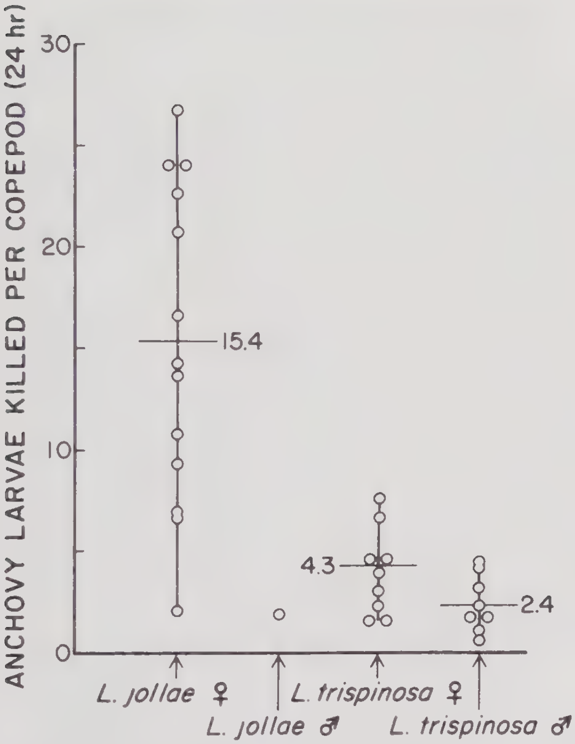

FIGURE 8.—Predation by individual *Labidocera jollae* and *L. trispinosa* under comparable prey density. Experiments were conducted in the dark for 24 hr in 3500 ml. Each circle represents the results of one experiment. The horizontal bar is the mean value for each series of experiments.

long when it hatches from the egg. Yolk-sac anchovy larvae have unpigmented eyes, lack a mouth and gills, and the yolk is invested with lipid (Bolin, 1936); when newly hatched the anchovy larva is very slightly buoyant. The newly hatched larva remains motionless most of the time at this stage and swims only sporadically. As it develops, swimming activity increases, occurring about 5% of the time at hatching to 25% on the second day and 50% by the third (John R. Hunter, personal communication). Figure 9 indicates a rapid decline in predation in the dark by *L. trispinosa* and *L. jollae* females as the larva grows older, presumably as a result of the latter's increased swimming and sensory ability. Effective predation is restricted therefore to yolk-sac larvae.

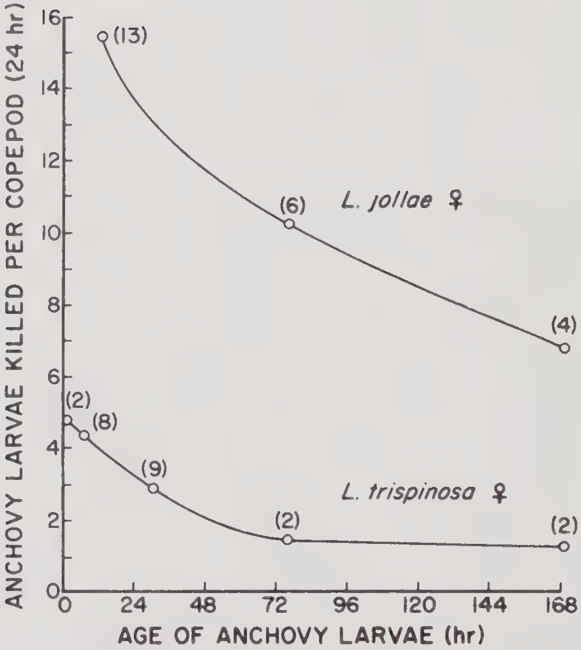

FIGURE 9.—The effect of the age of the anchovy larva on predation by *Labidocera jollae* and *L. trispinosa* females. Each open circle is the mean of the number of experiments shown in parentheses. The age of the larva at the beginning of each experiment is given on the abscissa.

EFFECT OF LARVAL ANCHOVY DENSITY ON *L. jollae* PREDATION

Given 2 to 3 days, single *L. jollae* females can kill by capture or biting all of 30 young anchovy larvae in 3500 ml. This is shown in a mortality curve (Figure 10) constructed from the results of a series of experiments, each of which had a number of newly hatched larvae (30 or less) at the start confined with a single *L. jollae* female. The density of larvae per unit volume (within the limits of these experiments) seemed to have little or no effect on the kill rate until there was only one larva remaining per 700 ml, when the rate due to predation by the copepod declined drastically. Our experience with predation experiments in 3500 ml volumes suggested that anchovy larvae were randomly distributed in this relatively small volume and that in the dark, at least, each *L. jollae* female could almost

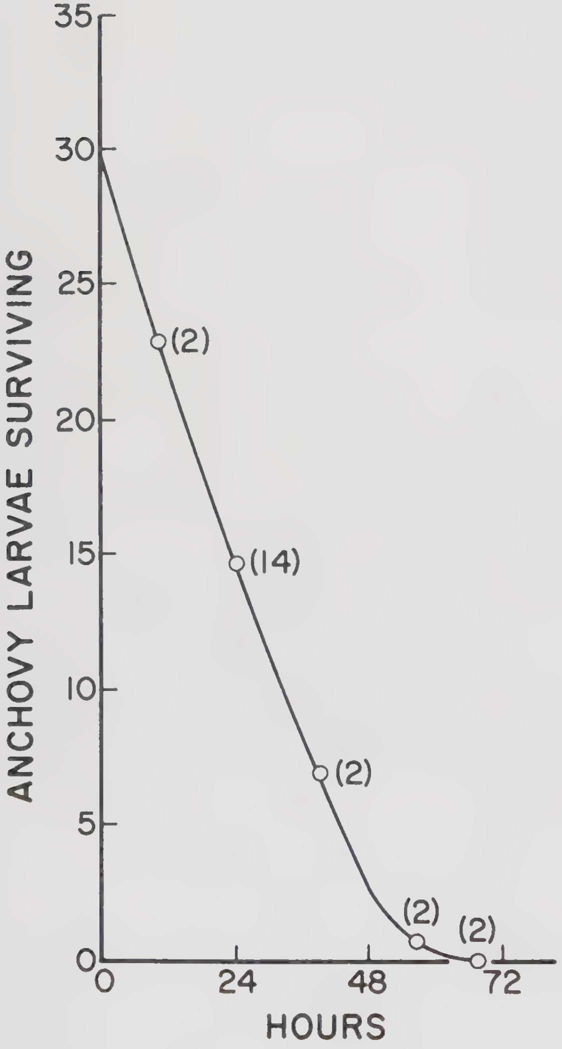

FIGURE 10.—Survival of 0- to 1-day-old anchovy larvae in the presence of a single *Labidocera jollae* female. The curve is a composite from a series of experiments in 3500 ml starting at different larval densities per copepod where the time was noted after the capture of a number of larvae. The numbers in parentheses indicate the number of experiments ending at each point.

completely search half this volume in 24 hr, resulting in continuing random contact with and killing of most, although not all, of the suspended larvae when two or more *L. jollae* females were present.

THE EFFECT OF AN ADDITIONAL PREY ON LARVAL PREDATION BY *Labidocera*

Recent experiments by Brooks (1970) with *Labidocera trispinosa* showed that this copepod selects *Artemia salina* nauplii over copepod nauplii from the plankton. She concluded that *Artemia* nauplii are selectively grazed because they are relatively less mobile, hence more easily captured.

We tested predation by *L. trispinosa* on *Artemia* nauplii and found that grazing corresponded roughly to the results we obtained when fish larvae alone were killed, i.e., up to a certain concentration all *Artemia* nauplii were killed in the experimental container in the dark over 24 hr. Survivors were found only if the number of nauplii exceeded 11-14 nauplii/liter/copepod. As the density of nauplii was increased more were killed. This result was the same whether experiments were performed in 3500-ml beakers or in 200-ml Petri dishes (Figure 11).

When *Artemia* nauplii in various concentrations and 30 anchovy larvae were offered together to five *L. jollae* males or five *L. trispinosa* males or females, larval mortality decreased in

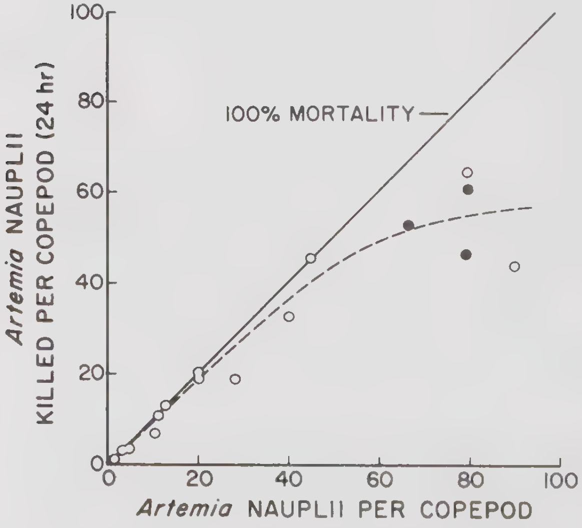

FIGURE 11.—Mortality of *Artemia* nauplii due to *Labidocera trispinosa* female predation at different densities of nauplii per copepod. Closed circles indicate experiments done in 200-ml Petri dishes.

proportion to the number of *Artemia* nauplii present. The results of these experiments are shown in Figure 12. There was a 50% decrease in mortality of larvae with *L. trispinosa* females, *L. jollae* males, and *L. trispinosa* males when the nauplii concentration was approximately 220, 150, and 100 nauplii/liter, respectively. The decrease in larval mortality is accentuated if *Artemia* nauplii are offered to *Labidocera* when older larvae are present. Fewer *Artemia* nauplii need to be present to depress the predation mortality on older larvae (Figure 13). The ease with which *Labidocera* can capture *Artemia* may make it less likely that fish larvae will be attacked. As the larvae age, this effect is compounded since it has become even more difficult to catch larvae and hence relatively less taxing for the copepod to take *Artemia* nauplii.

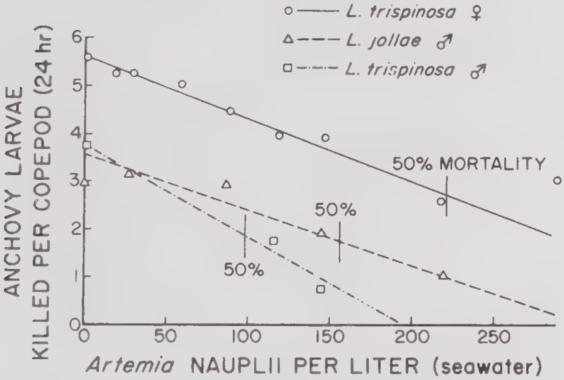

FIGURE 12.—Predation by *Labidocera jollae* males and both sexes of *L. trispinosa* on anchovy larvae when *Artemia* nauplii were also available to the copepods. Fifty percent reduction in larval mortality occurred when *Artemia* nauplii numbered 220/liter with *L. trispinosa* females, approximately 150/liter with *L. jollae* males and 100/liter with *L. trispinosa* males.

CALORIC REQUIREMENT OF *L. jollae* AND *L. trispinosa*

We noted that the vigor of *Labidocera* individuals declined with time if they were not fed or fed only *Artemia* nauplii. For example, after 1 week in the laboratory the activity of copepods fed only *Artemia* was diminished so that a copepod's ability to capture larvae was about one-half that of a newly caught copepod. *Labidocera* died after 2 or 3 days of starvation. This was preceded by a decrease in swimming activity which was reflected in a lower respiration rate and dry weight of individuals. In Figure 14 we give comparative respiration rates and dry weights for *L. jollae* females (a) newly caught, (b) larval-fish fed, and (c) starved for 2 days. These results show an enhanced respiratory rate for fed and presumably healthier animals and a drastic decline due to short term starvation.

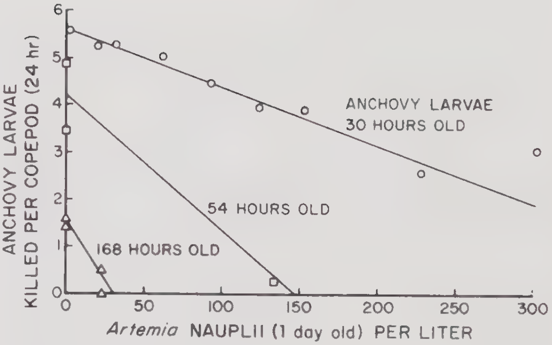

FIGURE 13.—The effect of the age of the anchovy larva and the addition of an extra prey (*Artemia* nauplii) on larval mortality due to predation by *Labidocera trispinosa* females.

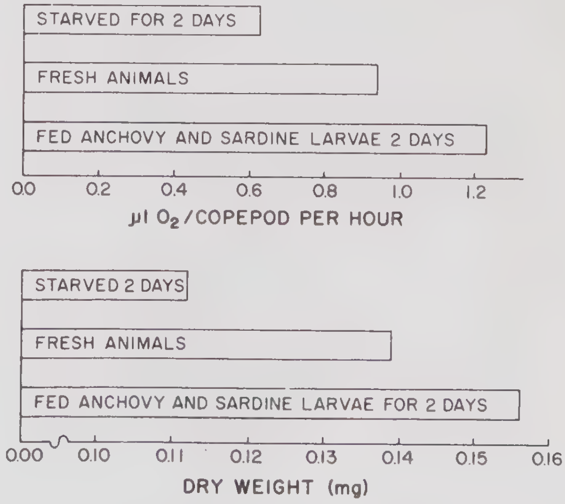

FIGURE 14.—Comparative oxygen consumption and individual dry weight measurements of *Labidocera jollae* females under starved and well-fed conditions at 18° C.

Further comparisons of respiration rates were made only between newly caught and larval-fish fed *L. jollae* females, males, and *L. trispinosa* males and females (Figure 15). In each instance there was an increase in respiratory rate after feeding on anchovy larvae. The caloric requirement of *Labidocera jollae* and *L. trispinosa* was calculated from oxygen consumption data to estimate the number of larvae which could sustain the copepod in a healthy condition at 18° C (Table 1). In spite of *Labidocera's* ability to kill large numbers of fish larvae or *Artemia* in a day, actual caloric requirements may be met by ingestion of only a few (1-4) larvae or nauplii (4-16).

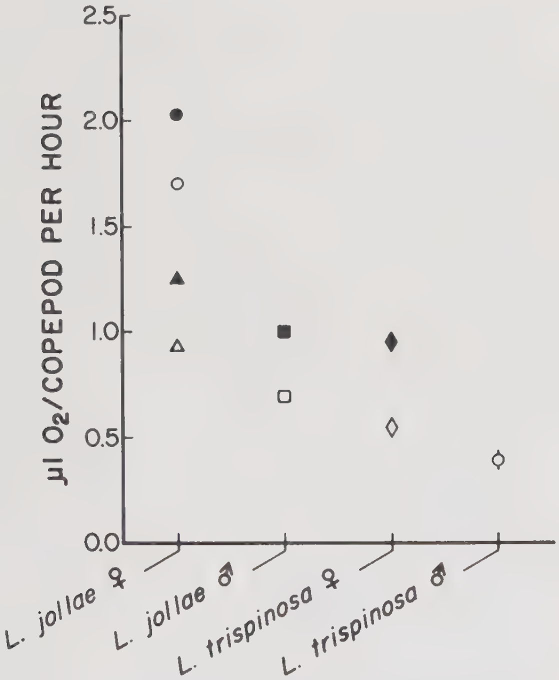

FIGURE 15.—Oxygen consumption by newly caught (open symbols) and larval-fish fed (closed symbols) labidocerans at 18° C.

PREDATION ON FISH LARVAE AND *Labidocera* BY *Pontellopsis occidentalis*

Pontellopsis adults and copepodites stages IV and V can kill by biting or capture and ingestion of anchovy larvae; older larvae (up to 3.5 days old in our test) were killed by this copepod as easily as yolk-sac larvae. Each stage V copepodite killed three larvae per day on the average and each adult female killed about 11 per day (Figure 16). We observed also that *Pontellopsis* attacked and ate *Labidocera* spp. when they were confined to the same beaker.

CO-OCCURRENCES OF PREDATORY COPEPODS AND FISH LARVAE IN THE SEA

In the laboratory we noted that 30 to 40% of the *Labidocera* individuals resided in the upper 5 to 25 cm of 140-cm-deep, 17.5-cm-diameter tanks—both in darkness and in the light. Yolk-sac anchovy larvae occupied a similar stratum because they are slightly buoyant. In the sea, spawning by anchovies occurs mostly in the upper 10 m but occasionally may occur relatively deeply (Ahlstrom, 1959). This prompted us to

TABLE 1.—Oxygen consumption and the calculated number of anchovy larvae required to sustain the respiratory requirements of *Labidocera jollae* and *L. trispinosa* per day at 18° C. The oxycalorific equivalent of 1 µliter of oxygen is 0.005 calorie. Yolk-sac anchovy larvae weigh 0.01 mg dry weight and contain 0.054 calorie. These data assume 100% digestive assimilation and an $RQ = 0.8$ for each copepod. Approximately four *Artemia* nauplii are calorimetrically equivalent to one anchovy larva.

Species and sex	$Q\ O_2$ µliter/mg dry weight/hr	O_2 consumption µliter/copepod/hr	Average dry weight per copepod (*mg*)	Anchovy larvae required/day
Labodocera jollae ♀	11	2.0	0.19	4
L. jollae	11	1.0	0.095	2
L. trispinosa ♀	7.7	0.96	0.12	2
L. trispinosa	4.3	0.40	0.092	1

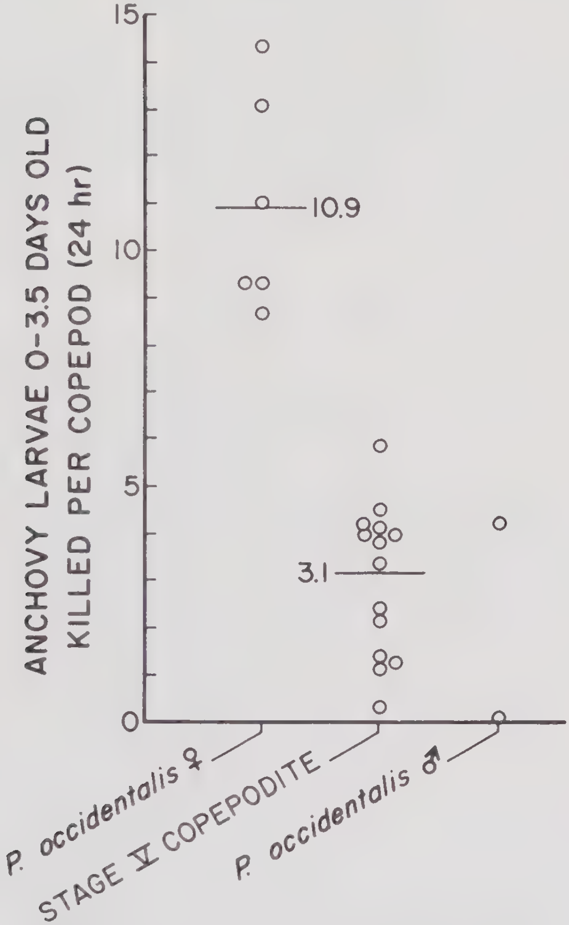

FIGURE 16.—Predation by *Pontellopsis occidentalis* on anchovy larvae 0 to 3.5 days old. Each horizontal line indicates the mean value of the experiments shown with open circles; 30 larvae were provided to 1 to 6 copepods in 3500 ml at the beginning of each experiment.

measure the rate of ascent of anchovy eggs to determine the maximum depth at which spawning could occur and yet insure the presence of yolk-sac larvae at the surface. In La Jolla seawater, salinity 33‰ and 17° C, anchovy eggs rise 5 cm/min or 3 m/hr. Thus, with time from spawning to hatching at 2 days, eggs spawned as deep as 144 m would hatch at or near the surface of the ocean, although spawning that deeply is rare (Ahlstrom, 1959). During development and, as they use up their yolk, anchovy larvae become almost neutrally buoyant and start to sink very slowly in laboratory containers. Even so, after 2 days of development, 50% of the laboratory-reared larvae were still above the 30 to 40 cm depth.

Ahlstrom (1959) reported closing-net captures of anchovy larvae at a variety of stations and depths in the California Current off California and Baja California. He has kindly provided us with length distributions of anchovy larvae taken at two stations, a night station, 5206-90.28, where over 500 larvae were taken, and a day station, 5504-120.50, where over 5000 larvae were captured. The length of the larva is roughly indicative of its age (Kramer and Zweifel, 1971), and we have tabulated the depth distribution of anchovy larvae at these stations by length and age (Table 2).

The depth distributions by age and length of anchovy larvae indicate that 50% or more of anchovy larvae up to 3 weeks old are above 10 m in depth. Fifty percent of the youngest class, 3 to 4.5 mm and 1 week old or less, were above 3.5 m during the day, and were slightly more than 2 m deep in the night. Ahlstrom's data also suggest that larvae of the Pacific sardine, *Sardinops caerulea*, Pacific mackerel, *Scomber japonicus*, and jack mackerel, *Trachurus symmetricus*, all pelagic fish of the California Current, may be similarly distributed.

Labidocerans are not diurnal vertical migrants and seem to be confined near the surface of the sea. Oblique tows with a plankton recorder (Longhurst et al., 1966) were taken in an area where *Labidocera trispinosa* and anchovy larvae are known to occur. The results are shown in our Table 3. The volume of each discrete sample at a particular depth was small (4-6 m^3) and the zeros may simply indicate relatively low abundance below the surface. Both tows, taken a day apart in close proximity to one another, showed that *L. trispinosa* was mainly present above 10 m, as were anchovy larvae. Simultaneously 10-min neuston tows were taken which filtered 463 m^3 no deeper than 30 cm at the surface of the sea (Table 4). The large number of *Labidocera trispinosa* and anchovy larvae in these tows suggests that the upper 30 cm of the ocean

TABLE 2.—Depth distribution of anchovy larvae by age and length at two stations, 5504-120.50 (day) and 5206-90.28 (night); collected by Ahlstrom (1959).

Average depth of catch (*m*)	Length and age of larvae							
	3.0-4.5 mm 0-7 days old		5.0-7.5 mm 8-14 days old		8.0-11.0 mm 15-21 days old		11.5+ mm 21+ days old	
	no.	% of total	no.	% of total	no.	% of total	no.	% of total
Station 5504-120.50 (day)								
2	515	42	505	17	283	37	64	36
7	317	26	820	28	216	28	52	29
18	138	11	596	20	78	10	31	17
27	96	8	138	5	31	4	5	3
44	105	9	509	17	62	8	19	11
60	61	5	324	11	95	12	7	4
74	1	0	70	2	1	0	0	0
Total	1233		2962		766		178	
Station 5206-90.28 (night)								
2	65	50	52	40	44	20	35	36
7	54	42	48	37	73	34	25	26
17	10	8	15	12	50	23	14	14
27	0	0	15	12	49	23	23	24
Total	129		130		216		97	

TABLE 3.—Vertical distribution of *Labidocera trispinosa* adults and anchovy larvae at 32°55.1′ (Station 1 at 0100) June 3, 1970, and 32°45.8′ (Station 2 at 2340) June 3. Volume of water filtered for each discrete depth sample in oblique tows were: Station 1, 6 m^3; Station 2, 4.35 m^3. No *L. jollae* or *Pontellopsis occidentalis* individuals were caught in these samples.

Depth (*m*)	Number of *L. trispinosa* adults	Number of *Engraulis mordax* larvae
Station 1		
0- 3	13	5 (7-11 mm long)
3- 7	0	1
7-15	0	1
15-60	0	0
Station 2		
0- 2	4	17 (7-10 mm long)
2- 7	17	11 (9-10 mm long)
7-15	2	1
15-25	0	1
25-60	0	0

TABLE 4.—Numbers of *Labidocera jollae, L. trispinosa, Pontellopsis occidentalis*, and *Engraulis mordax* eggs and larvae taken in 463 m^3 within 30 cm of the surface simultaneously with the oblique tows described in Table 3.

Species	Station 1	Station 2
L. trispinosa	1152	6400
L. jollae	336	104
P. occidentalis	112	128
E. mordax	226 (5-10 mm long)	36 (10-12 mm long)

is the area which should be examined for further elucidation of this predator-prey relationship.

The observations presented in this paper indicate that marine copepods may be effective predators on larval fish, at least in the sense that a predator need not devour its prey but is equally effective if it injures it mortally. Young pelagic fish larvae are particularly susceptible to biting zooplankters because they have an extremely thin skin and are unable to survive once the skin is punctured. Pontellid copepods, in particular *Labidocera* spp., appear to have a well-developed vibration sense which serves to orient the copepod toward its swimming prey although this is preceded by random searching. A fish larva with its beating tail provides the right stimulus to the copepod to initiate an attack when the latter is close enough to detect the beat.

We have called attention to the vertical distribution of *Labidocera* in the sea and the apparent co-occurrence of larval anchovies in the same depth stratum. Unfortunately, quantitative data on the density of predatory copepods or other zooplankters as related to fish larvae have yet to be made. It is our opinion that pontellid copepods and fish larvae are concentrated in the upper few meters and probably the upper few centimeters of the sea and that observations of this oceanic fine structure may reveal densities of fish larvae to copepods which would implicate predatory copepods (and possibly other zooplankters) as important causes of larval fish mortality.

ACKNOWLEDGMENTS

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THE CLUPEOID RESOURCES OF TROPICAL SEAS

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INTRODUCTION

The world catch of fish from the sea has doubled in the last decade, rising from $24\cdot1 \times 10^{6}$ tons in 1958 to $49\cdot7 \times 10^{6}$ tons in 1968 (Anonymous, 1969); in this period the catch of clupeoid fish has expanded at an average annual increase of 11·8% from 7·2 to $20\cdot5 \times 10^{6}$ tons, which is significantly greater than the 6·3% annual increase for other sorts of fish. Much of the increased exploitation has fallen upon the clupeoid stocks of lower latitudes; during this period the catch of high latitude herrings (*Clupea* spp.) has increased only from 3·2 to $4\cdot0 \times 10^{6}$ metric tons annually, while the clupeoids of warmer seas have sustained a fourfold increased rate of exploitation from 4·0 to $16\cdot0 \times 10^{6}$ metric tons annually. The clupeoid catch is mostly used industrially in the production of fish meals and oils and the increased catches have been in response to an expanding demand in world markets for these products; thus, as the percentage of the world catch composed of clupeoids has risen, so has the percentage of the total world catch which is used industrially; in 1948 only 7·7% was so used, rising to 13% in 1958 and to 35·6% in 1968. The warm-water clupeoids contributed very largely to this spectacular increase in industrial production. About $4\cdot66 \times 10^{6}$ tons of fish meal were manufactured in 1968 to which the catches of *Sardina*, *Sardinops*, *Sardinella*, *Brevoortia*, and *Engraulis* contributed $3\cdot05 \times 10^{6}$ tons, while high latitude fisheries for *Clupea* contributed only $0\cdot76 \times 10^{6}$ tons; the remaining $0\cdot85 \times 10^{6}$ tons were made up of non-clupeoid species.

There is no indication that the industrial demand in the developed countries of the world for fish meal, fish oil, and solubles will decline; indeed, forecasts indicate an increasing demand for such products as industrial farming extends its scope, and as the range and use of formulated human foods requiring the use of proteins of high biological acceptability continues to increase. It seems probable that fish meal and more highly-refined fish protein concentrates will continue to be competitive with proteins of plant origin in at least part of the industrial protein market. There are also indications of considerable under-utilization of some tropical clupeoid stocks and while, to be sure, no second event to rival the boom-years of the Peruvian fish meal industry can be looked for, significant growth in catches may reasonably be anticipated for several decades.

It has seemed appropriate, therefore, to review briefly what is known of the biological basis of tropical fisheries for clupeoids; the term 'tropics' is here interpreted very loosely and fisheries will be discussed in latitudes as high as is necessary to explain the biology of low latitude species and their exploitation.

SYSTEMATICS AND DIVERSITY OF FORM

The clupeoid fish are small teleosts which are relatively 'unevolved' and typically are less than 20 or 30 cm in length; they have no barbules and are frequently laterally compressed, with a series of hard scutes along the ventral surface of the body. Most are soft-bodied, difficult to handle, and covered with rather deciduous scales. Most species are greyish or silvery in colour and usually the only patterns on the body are those for counter-shading, making them inconspicuous in the sea; related to their inconspicuous coloration is their very frequent habit of occurring in schools, sometimes very large ones. Their flesh is often very oily, and the oil content normally varies seasonally, even in low latitude species. According to Berg's classification, the Order Clupeiformes includes many fossil suborders as well as several suborders containing living members as diverse as the herrings and the salmon-like fish. The suborder Clupeoidei includes several groups of families of herring-like fishes: the Elopoidae and Albuloidae, containing carnivorous, large, silvery tropical sea fish; the Alepocephaloidae, containing small abyssal and bathypelagic fish; and the Clupeoidae, with which we are concerned in this review, and to which reference is intended by the general term 'clupeoid'. There are two Families of living clupeoids: the herrings and their relatives of the family Clupeidae, and the anchovies of the family Engraulidae. The herrings are larger, more diverse in form, and extend into higher latitudes than the smaller anchovies, which are characterized by their very long maxillae and lack of a lateral line. Many members of both families have reduced dentition and an abundance of filamentous gill rakers. The great majority of the several hundred species of clupeoids occur in warm or tropical seas. While only a single genus (*Clupea*) is important in high latitudes and the cold temperate regions, in the warm temperate mid-latitudes there are approximately 10 important genera, dominated by *Sardina*, *Sardinops*, *Engraulis*, *Brevoortia*, *Ethmidium*, *Opisthonema* and others. In low latitudes more than 25 genera occur, many of which are important.

The general rules governing the diversity of animal life in high latitudes and low, in eutrophic and in oligotrophic regions, and in stable and in varying environments, have been demonstrated in many animal groups. It is evident that clupeoid fishery resources follow similar rules with regard to variation in their diversity; in high latitudes where the oceanographic regime varies widely from winter to summer, and where there is a spring bloom of diatoms followed by a peak of zooplankton, there are relatively few species of clupeoid fish. In low latitudes, where the seasonal changes in food supply and the level of the standing crop of food is lower, the diversity of clupeoids is high. This latitudinal trend is broken, in the tropics, in situations where local seasonal upwelling occurs; here, a few species of clupeoids may occur in great abundance, their biomass dominating the total fish biomass of the area; it is in such situations that the great clupeoid fisheries of low latitudes occur and which, moreover, are based to a considerable extent upon species which are specialized phytoplankton-feeders.

Not all zoogeographical regions have, at similar latitudes, a comparable diversity of clupeoids; the paucity of the tropical marine fauna of the Gulf of Guinea compared with the equatorial regions of the western Atlantic is well known (e.g. Ekman, 1953) as is, in general, the even greater diversity, habitat for habitat, of the Indo-Pacific equatorial region than the Atlantic. The clupeoids appear to follow the same patterns with the consequence that all types of clupeoid ecology do not occur in all tropical oceans. The menhadens of the western boundary currents of the Atlantic and the bonga of the tropical regions of the eastern Atlantic are extremely close to each other both morphologically and in their ecology, and it is not clear why there are no *Brevoortia*-like fish in the truly tropical regions of the western Atlantic, nor why menhaden or bonga-like forms are not widespread in the shelf regions of the western Indo-Pacific, where conditions would appear to be extremely suitable for their development. With this possible exception, the western parts of the Indo-Pacific region include the richest diversity of clupeoid ecology and this area is particularly rich in the large number of predacious *Ilisha*-like forms which occur there, while at the other end of the scale the west African region of the eastern tropical Atlantic exhibits a very reduced diversity of clupeoid ecology; here there are no round herrings (*Dussumeria*), there are no gizzard shads (*Dorosoma*), and there are no toothed anchovies (*Lycengraulis*, *Lycothrissa*, *Coillia*). Only a single species of predatory herring (*Ilisha africana*) occurs in the eastern Atlantic, compared with the many genera, including tens of species, of this ecological type in the western Indo-Pacific.

ECOLOGY

TOLERANCE OF LOW SALINITIES

With few exceptions, clupeoids occur over or near the continental shelves and frequently their habitat is strictly coastal; associated with their neritic distribution is a rather widespread tolerance of low salinities, though not all species are euryhaline. Within single genera, such as *Sardinella*, a rather wide range of tolerance to salinity changes may occur. The tropical Atlantic *S. aurita*, for example, is extremely stenohaline, tolerating only a very small range in the salinity of its environment; Postel (1955) shows that it does not occur in water with a salinity lower than 35‰, so it does not enter estuaries and avoids those parts of the coast which are much influenced by terrestrial run-off. In the Gulf of Guinea it is confined to rather restricted parts of the coastline. On the other hand, *S. cameronensis* occurs mainly in the Bights of Benin and Biafra, where mixed-layer salinities regularly fall as low as 20‰; *S. eba*, the third West African congener, occurs widely along the tropical coastline where it frequently enters estuaries and coastal lagoons. A similar series of congeneric species with stenohaline and euryhaline habits could probably be demonstrated for the same genus around the coasts of India (i.e. among *S. longiceps*, *S. gibbosa*, *S. albella*, *S. sirm*, and *S. fimbriata*) and elsewhere in the tropical seas.

The euryhaline species of both tropical and temperate latitudes include shad-like forms which are anadromous, entering fresh water and frequently penetrating far up rivers during their spawning migrations, as well as species which do not regularly migrate between brackish and marine environments. The most familiar shads are the species of *Alosa*, which enter rivers in large spawning runs on the North American continent. These, together with the gizzard shads (*Dorosoma*) and the alewives (*Pomolobus*) are replaced in the Indo-Pacific region by river-ascending shads of the genera *Hilsa* and *Macrura*. In the tropical Atlantic there appear to be no important shad-like fishes in the large tropical rivers of western Africa. This is perhaps another facet of the general poverty of the tropical Atlantic marine fauna compared with that of the Indo-Pacific, and one which invites consideration of planting such species to enrich the fauna available for fisheries.

Among the anchovies of the family Engraulidae, several genera occur only in tropical fresh waters. Perhaps the most important of these are species of *Lycengraulis*; for example, *L. grossidens* occurs in western South America from Venezuela to Rio de Janeiro, where it is important in local markets, and ascends quite small streams. Another member of the same genus (*L. limnichthys*) occurs only in Lake Maracaibo in Venezuela. The genera *Pterengraulis* and *Hildebranchichthys* are also found in the Amazon basin and Venezuela where, again, they are very commonly caught in local indigenous riverine fisheries. Turning to the herring-like species of Clupeidae, we find a rather smaller number which are adapted purely to low salinity environments; there are, of course, some cases in which anadromous shad-like forms have become landlocked and invaded fresh waters within recent times, the best-known example of which is the invasion of the Great Lakes of North America by the alewife, *Pomolobus aestivalis*, whose range previously included only the rivers between Nova Scotia and North Carolina. In South American rivers, the genus *Rhinosardinia* is restricted to fresh water, while in West Africa the little *Pellonula vorax* does not descend below upper estuarine conditions. In the Indo-Pacific region, species of *Pterothrissa*, *Microthrissa*, and *Pellonula* are among those restricted to waters of very low salinity, or to riverine conditions. Land-locked species may represent important fishery resources. In Lake Tanganyika, in the African Rift Valley, two small clupeoids are abundant, namely, *Stolothrissa tanganicae* and *Limnothrissa miodon*. Hickling (1961) describes the fishery in the open lake for the first of these two species, which is a pelagic, zooplankton feeding fish that can be attracted in enormous numbers to lights at night, and whose potential catch has been estimated at more than $1{\cdot}0 \times 10^5$ tons annually.

SCHOOLING HABITS

One of the most significant characteristics of clupeoids from a behavioural and also from a fisheries viewpoint is their occurrence in dense and often very large schools which containing many hundreds of thousands of fish may weigh up to more than 100 tons in some cases. Such large schools generally occur in the open ocean rather than in restricted brackish waters and frequently have a shape and type of behaviour which is diagnostic and which enables an experienced fisherman to identify them. This may be done either by direct observation from a fishing vessel, by observation from a light airplane, or by the use of hydro-acoustical instruments, such as echo-sounders and sonars. The specific diagnosis of a school is generally made on a combination of factors. Its size, the depth at which it is swimming, the shape it makes in the water, the manner in which the individual fish break the surface (if this occurs), and the colour of the mass of fish as they glint in the sun, may all be taken into account. Furthermore, at night, the schools of some species may be readily visible and identified even at some depth in clear water when there is significant bioluminescence from the plankton; under these conditions the individual shoals may appear as large balls of green fire deep in the water—a sight once seen, never to be forgotten.

In the Gulf of Guinea, canoe fishermen recognize bonga, *Ethmalosa dorsalis*, by their habit of flipping on their sides and breaking the surface when feeding—each fish sending up an individual little splash, these splashes being rather widely scattered across the area occupied by the school; when not feeding, *Ethmalosa* at sea are distinguished rather easily from the several species of *Sardinella* which are found in the same region, since the golden glint of each individual fish gives a reddish tinge to the whole shoal when it is seen from far off (Postel, 1955). On the other hand, *Sardinella* in the same region normally form a dark bluish ‘stain’ at the surface, and the schools are apparently far more compact and closer to the surface so that they break it in a manner resembling the beat of rain on water; this is quite unlike the way *Ethmalosa* breaks the surface (Postel, 1955). The migrating shoals of the western Atlantic species of menhaden (*Brevoortia* spp.) have a very characteristic form and are seen dark against the background of the sea surface from the small spotter aircraft used by the fishery of the eastern seaboard of the United States; migrating shoals of thread herring (*Opisthonema* spp.) in the same region can usually be distinguished by the spotters from the menhaden which they are seeking. Shoals of *Brevoortia* and some species of anchoveta have another important diagnostic character in shallow-water feeding areas, where mud ‘boils’ covering several hectares of sea surface are formed by the activity of the fish; such boils are easily seen by spotter aircraft which may direct fishing vessels onto them.

The function of the schooling habit in clupeids is to be found in the relationship between predator and prey; not only are aggregations of individuals more difficult for a more widely dispersed predator species to locate but, once located, incorporation within a tight school protects the individual fish by means of the visual confusion it offers to the predator. Discussing the schooling of small fishes in open environments which are the prey of larger, more solitary predators, Brock and Riffenburgh (1960) showed that there is an “encounter advantage” in schooling which expresses the fact that by random searching a predator has a smaller chance of encountering an aggregated than a dispersed prey. On the other hand, once encountered, a large school may be at a detection disadvantage compared with a small school—it is easier to detect, once the predator is in its general area. Once the final contact between predator and prey has been established, and ignoring the problem of visual confusion of the predator, it may be assumed that a smaller percentage of a large school will be required to satiate a predator so that the individuals within it have a better chance of escaping at each encounter.

The capture of a small fish by an active, visual predator involves a complex behaviour pattern on the part of each; the predator must visually identify its prey, follow it during its escape activities, and finally take it. This pattern of predation cannot occur if the initial identification of the prey individual can be prevented, and this is perhaps the main function of tight schools of fish normally preyed upon by other fish (Hunter, pers. comm.). Anybody who has attempted, with a small hand net, to capture one goldfish from a tank full of goldfish or one bird in an aviary full of fluttering birds, knows how much easier this task becomes as the number of individuals, from which the captured individual has to be selected, is progressively reduced. There are many observations which indicate the correctness of this supposition and which demonstrate that very frequently the prey individuals which are successfully captured are those which do not, for some reason or other, remain within the coherent pattern of the school, but stray to one side; the initial dash of a predator into the thick of a school may not be so much intended to capture an individual prey as to break up the coherence of the school and to separate one or more individuals from it by their flight reaction, and subsequently to capture them. The behavioural patterns within clupeoid schools are rather rigid, are effective in passing information rapidly from individual to individual concerning the whereabouts of predators, and probably result in the tightening of the school under attack to prevent individuals being cut out of its pattern. Clupeoid schools are usually more or less on the move; during their passage through the water, a densely packed school may leave a trail as distinct as that left by a flock of sheep crossing an untrodden meadow. In the wake of a large shoal of anchovies, for instance, one may see the effect of intense and massive filtration upon the plankton content of the water and also a train of oil droplets rising to the surface resulting in a fish-oil slick. The functions of the schooling habit among clupeoids and its advantages for the species compared with a dispersed type of distribution, are probably various, but it seems certain that the most important is that of making the task of a predator more difficult.

Many tropical species apparently perform duel vertical migrations; this has been well demonstrated for the North Atlantic herring *Clupea* (e.g. Brawn, 1960), and has also been shown for a number of tropical species, such as *Sardinella aurita* off the coast of Ghana (Probatov, 1959). It is also apparent from sonar observations of some species, including the Californian anchovy, *Engraulis mordax* ,that shoals may disperse at night into small groups of fish (Smith, pers. comm.), and it has been suggested that in this way the groups of anchovies act at night, during their feeding activities, as predators in the predator/prey model of Broch and Riffenburgh (Hunter, pers. comm.). At dawn the small parties of perhaps five to ten individuals coalesce and the schools reform.

The seasonal migrations of clupeoids have an important effect upon the fisheries, particularly upon unmechanized fisheries which must by their nature be restricted to certain locations. The European–Scandinavian herring, *Clupea harengus*, is a particularly well-documented example of a migrating clupeoid in high latitudes, as is the Indian oil-sardine (*Sardinella longiceps*) in the tropical seas. Mass migrations of such species frequently result in the fishery being strongly seasonal in nature and this is of particular importance where the nature of the social and economic structure of the fishery prohibits its operating over long distances, and so following the migrations of the species to whose capture it is specialized. It may be a question of waiting for the return of the fish each year along their accustomed migration routes, rather than migrating with the fish, as did the traditional fishery for the North Sea herring in the British Isles in which the Scottish fishing boats, and the girls ashore who cleaned the herring for the salting-down process, followed the fishery progressively southwards during the year from Scotland to East Anglia. Factors such as this are important, but are often neglected, in fisheries development plans in the tropics.

FEEDING REGIMES

With a few, but interesting, exceptions the clupeoids are microphagous, that is, their food is of small particle size. Predominantly, they are plankton-feeders, but they include a number of important species whose diet is particularly dominated by phytoplankton; they tend, therefore, to be rather 'low' in the food web in the sea, being close to the primary producers and this, of course, has significance in the very great productivity of clupeoid fisheries.

Leaving aside the few macrophagous forms such as the wolf-herring (*Chirocentrus*), the tarpon (*Megalops*), the ten-pounder (*Elops*), and the ladyfish (*Albula*) which are large, active fish-eating predators that are ecologically and systematically rather distinct from the true clupeoids, several clupeoid genera contain species whose adults have a diet in which relatively large crustaceans and small fish figure largely; these are the exceptions to the general rule of microphagy within the clupeoids. They include: the small, tropical, large-toothed, anchovy-like forms such as *Lycengraulis*, *Lycothrissa*, and *Coilia*; a number of genera of soft, very flattened herring-like forms having upturned toothed mouths, such as *Ilisha*, *Pristigaster*, *Opisthopterus*, *Raconda*, *Pliosteostoma*, and *Odontognathus*, all of which are restricted to low latitudes (e.g. Peterson, 1956). Some species of the thread herring, *Opisthonema*, and the warm-temperature shads of the genus *Pomolobus* have similar diets but are not so restricted to the tropical zone. The great majority of the clupeoids, on the other hand, have a diet which is based on zooplankton, mainly copepods and other small crustacea, and in which the adult fish occur often in more organized and denser schools than do the macrophagous genera mentioned above. These are characterized by the boreal species of *Clupea* and *Sprattus* whose ecology is well known on the coasts of Europe and North America. In the tropics there are several genera so close to *Clupea* in form and ecology as to be commonly known as tropical herrings; most species of the wide-spread genus *Sardinella* (Vijayaraghavan, 1953; Bainbridge, 1963) fall into this category, as do *Harengula*, *Clupeoides*, *Jenkinsia*, and *Lile*. The tropical round-herrings, widely distributed in the Indo-Pacific also have diets based mostly on macrozooplankton and have a very generalized form of dentition; these include *Dussumeria*, *Spratelloides*, and *Etrumeus*. The smaller tropical anchovies (*Anchovia*, *Anchoa*, *Anchoviella*, and *Setipinna*) appear in general to have an unspecialized zooplankton diet as do many of the brackish water forms such as the warm-temperate shads *Alosa* and the tropical West African *Pellonula*.

The species which have a purely phytoplanktonic diet, or at least a diet in which phytoplankton appears to be the preferred component, feed by filtering large diatoms and other phytoplankters from the water by means of elongated gill rakers which form a filtration sieve. Though few in number, from a fisheries point of view these species are some of the most interesting, both because of their occurrence in great quantity and also because they represent the most efficient possible utilization of the results of primary production. The small anchovies *Engraulis ringens* and *Cetengraulis mysticetus* in the eastern Pacific (Bayliff, 1963), the menhadens (*Brevoortia* spp.) in the western Atlantic (Deevey, 1956; Darnell, 1958), the West African bonga *Ethmalosa fimbriata* (Bainbridge, 1960) and the Indo-Pacific thread herring *Opisthonema libertate* and oil-sardine *Sardinella longiceps* (Peterson, 1956; Nair, 1960), all fall into this category.

In a special category are the gizzard shads *Dorosoma* of tropical and mid-latitudes which, as their common name implies, utilize a strong gizzard, or muscular portion of the alimentary canal, to grind mud taken from the bottom of estuaries and shallow shelf areas, so as to utilize benthic diatoms. In this, their ecology resembles that of the grey mullets (see Thomson, 1966).

EASTERN ATLANTIC

In the eastern Atlantic the latitudinal range of tropical conditions in the ocean is rather small and is clearly separated by frontal regions from the eastern boundary currents (Canary, Benguela) to the north and south; within the tropical region—which corresponds approximately to the area known as the Gulf of Guinea and to the Guinea Current—there are smaller numbers of clupeoid species than in any other tropical area. High rates of primary production occur only in two situations: first, as Bainbridge (1960) has shown, there are very large standing crops of phytoplankton and very high rates of carbon fixation in shallow coastal lagoons and estuaries, throughout most of the year; secondly, off Ghana and the Ivory Coast there is an area of coastal upwelling, where high rates of primary production occur seasonally in August and September, and where enrichment also induces high standing crops of planktonic biota, which are different in specific composition from those of estuaries and lagoons. The centres of production of clupeoid fish, and hence of activity in fishing for them, follow the same pattern. In the estuaries and on those parts of the continental shelf over which estuarine conditions occur at least seasonally, *Ethmalosa fimbriata* forms the object of very important local fisheries; in the Ivory Coast–Ghana upwelling region, there are large and important canoe fisheries for the ‘herring’, *Sardinella aurita*, and also a recently developed industrial fishery for this and for *S. eba*. Also of interest to the West African fisheries is *Ilisha africana*, which is not so restricted to eutrophic areas and which occurs throughout the whole region and is a regular component of the demersal trawl catches on the West African continental shelf.

Ethmalosa fimbriata is both superficially and anatomically extremely similar to the western Atlantic menhadens (*Brevoortia* spp.), although Monod (1961) has shown by his anatomical study of the two species that this resemblance is rather a matter of convergence than of very close systematic relationship. Be that as it may, almost all that is known of the ecology of the American menhadens may be said to apply in general to *Ethmalosa*, which is a strong, active, filter-feeding clupeoid and attains a total length of approximately 40 cm. Bainbridge (1960) has shown that *Ethmalosa* obtains its food by passive filtration of phyto- and to a lesser extent microzooplankton with very little selection from the natural plankton communities by a detailed comparison of stomach contents and the catch in plankton nets hauled around the feeding school from which the fish were caught. Shoals of bonga are rarely found in clear water or far from estuaries or lagoons. In the Gulf of Guinea they occur in two regions: one, in the west, from Liberia to Senegal where many small rivers debouch and extensive estuarine and lagoon systems occur; the other, in the east, centred on the Niger Delta with its enormous lagoon systems and on the estuaries of the Cross and Cameroon Rivers. Although small populations occur off virtually every river mouth throughout the tropical region, bonga resources of importance occur only in these two major centres. *Ethmalosa*, like *Brevoortia*, spawns at sea (Bainbridge, 1960) and eggs and larval stages of this species have not been found in estuaries; however, within a few weeks of being spawned, the juvenile fish move into the estuaries in very great numbers and live there and in the lagoon systems, until they are approximately 10 cm in length, when they begin to migrate between the sea and the estuaries with a migration pattern similar to that of the adults (Salzen, 1958; Bainbridge, 1960). As Bainbridge (1960) has shown, there is a cycle of productivity and of standing crop of diatoms in these estuaries related to the tidal cycle; in brief, during periods of neap tide and small scour blooms of diatoms, principally *Coscinodiscus*, which appear to be flushed out in the intervening periods of spring tides and heavy tidal scour. The movements of *Ethmalosa* between the estuaries and the open shelf appear to be related to this cycle; during the neap tides and high crops of diatoms, the fish move into the estuaries to graze, returning to the shallow shelf areas outside the estuaries during periods of spring tides (Longhurst, 1960). Spawning appears to be more or less continuous throughout the year, although it is perhaps interrupted in June, July, and August by the effects of the rainy season when, due to the greatly increased flow from local run-off of the very heavy rains, 'neap tide' conditions scarcely occur in the estuaries. It is probable that a spawning peak occurs at the height of the dry season in January and February. As a result of this pattern, except during the rainy season when they appear to be flushed out, there are broods of young *Ethmalosa* from an inch or two in length constantly in the estuaries (Salzen, 1958); these juveniles appear to be restricted to the shallow parts of the estuaries where they fall easy and abundant victims to the fishing traps and to the large flocks of fish-eating birds, principally terns (*Sterna*), which also live in the estuaries especially during the dry season which is contemporaneous with the northern winter.

The fisheries for *Ethmalosa* follow the adult fish and are clearly dependent upon their pattern of migration; despite considerable effort to mechanize and modernize these fisheries by local fishery agencies and F.A.O., they remain to this day in an unmechanized state throughout most of West Africa. This is understandable because of the nature of the resource and of the environment of the fishery; it is scattered throughout a multitude of estuaries, lagoons, and inaccessible creeks and the fishermen live in thousands of small fishing villages and hamlets, most of which are accessible only by canoe or small launch and few of which are near a road.

This is a canoe fishery and some very fine canoes are deployed in it. The gear is of three kinds: most commonly, very large cast-nets are used during the day when the schools can be readily observed; in Sierra Leone, cast-nets of up to 18 ft in radius are used from seven-man canoes in which the caster (with two or three nets) stands in the bow, paddled by five paddlers, while the canoe is commanded by a captain who steers from the stern. The skill of these teams is quite extraordinary and one cannot but be impressed by the uncanny skill of the caster, who stands erect in the bow of a heaving canoe in a turbulent estuarine ebb-tide and throws a net which is undoubtedly one of the largest cast-nets developed anywhere in the world; on one occasion I counted as many as 250 *Ethmalosa* of 25 to 30 cm long in the catch from a single cast of such a net. More recently, small drift-nets have been used at night to take bonga in Sierra Leone, and the Ghanaian round-haul or 'ali' net, together with the typical Ghana canoes, has been introduced by migrant Fanti fishermen into the western bonga fisheries. In the fisheries of the eastern Gulf, particularly in Nigeria, the gear does not appear to be so evolved and smaller canoes and smaller cast-nets are the general rule; however, the small drift-net from two-man canoes at night is very commonly used in this region.

In Lac Nokoúe, in Dahomey, and in other eastern lagoon systems which have only very small or frequently-closed entrances through the beach, land-locked races of *Ethmalosa* appear to have developed; the species normally matures at about 21 or 22 cm in length and many adults attain at least 30 cm: however, in these lagoons the populations contain very few individuals longer than 12 cm in total length, and maturity first occurs at less than 10 cm. These populations are heavily fished by the lagoon fishing villages.

The *Sardinella* fisheries of the tropical West African coast are based upon two species, *S. aurita* and *S. eba*. These fisheries are concentrated in three regions: first, in the central upwelling area off Ghana and the Ivory Coast; secondly, in the frontal region, off Senegal and Casamance, between the Canary and Guinea Currents; and thirdly, in the frontal region between the northern Benguela Current and the tropical water of the Bight of Biafra, from Cape Lopez south towards the central Angola coast. In each of these areas, in the mid 1960s the total catch of *Sardinella* by canoes and small fleets of industrial sardine purse seiners was of the order of 50,000 tons (Zei, 1969). The composition of the landings between *S. aurita* and *S. eba* varies considerably from season to season and from place to place within these fisheries. *S. aurita* is quite unlike any of the other tropical east Atlantic clupeoids in form and ecology, being a long herring-like fish, very round in section. From the combined work of Postel and his associates in the French-speaking West African nations, of Johnson and others in the Ghana fisheries, and of the U.S.S.R. exploratory fishing surveys, there has now been built up a fairly satisfactory model of the biology and distribution of *S. aurita* off West Africa (Postel, 1959). It seems that this species alternates between periods spent in demersal schools in the offshore areas below the thermocline and others spent in surface waters and closer to the coast (Boradatov and Karpechenko, 1958). The species arrives off the coast of Ghana at the same time as the seasonal upwelling between June and late September; it feeds heavily during this period, as Bainbridge (1960) has shown, largely upon *Calanoides carinatus*, a copepod that dominates the zooplankton during the upwelling; while it is at the coast, *Sardinella aurita* is present in dense schools which can be seen at the surface and which are composed of maturing individuals. Spawning occurs towards the end of the upwelling period, after which the fish return to the deeper sub-thermocline waters farther offshore, and where they again occur in large demersal schools, that rise into mid-water and disperse slightly at night.

The dependence of the fishery upon the upwelling phenomenon and the consequent behaviour of the *Sardinella* is very clear, and in the rare years in which the upwelling fails, so does the fishery. In 1968, the rainy season in Ghana continued intermittently from June until October, and was not interrupted, as is usually the case, by a 'little dry season' caused by a high atmospheric pressure system, itself caused by a coastal upwelling process; in this year, too, the fishery was a complete failure (Kwei, pers. comm.). It may also be supposed that the 1968 year-class would have a high degree of probability of failure.

The same pattern is seen off Senegal and probably occurs also to the south of Cape Lopez, though this is less well-documented. The Soviet work to the south of Cape Verde (Boradatov, Karpechenko, Probatov and Biryukov, 1959) has shown that the schools are aggregated in the frontal region from July to September and include both one- and two-year old fish. During this period there is relatively little feeding, though the gonads mature rather rapidly and subsequently the fish move inshore to spawn. During the period of maturation, there are daytime demersal schools similar to those described by the Russians off Ghana and these show the same diurnal vertical migration. Movement towards the coast appears to take place in the mixed layer and Postel (1959) describes the schools immediately to the south of Cape Verde peninsula over the shallow parts of the continental shelf as being round in form when seen from above, dark in colour, fast moving, and breaking the surface like rain; he suggests that a school 15 or 20 m in diameter will contain 20 to 30 tons of fish and the largest will include about twice this quantity. The schools here foresake the surface and descend deeper in the mixed layer during the middle of the day; at this time they are easily located with a simple echo-sounder.

During the upwelling season off Ghana, when the onshore spawning movement brings such shoals to the surface and near to the coast, a seasonal herring fishery develops in the string of small fishing towns almost the whole length of the coast of Ghana; based on the great Ghanaian surf-canoes with their rounded section and high sheer at either end, the herring are taken by simple, round-haul nets worked from single canoes. Set around a 'breezing' shoal of herring, the net is not pursed completely, but by means of a great commotion in the middle of the set, the fish are induced to 'gill' themselves, and the net with its enmeshed catch is loaded back aboard the canoe. The fish can only be removed by spreading the net on the beach, and so canoes can make only a single catch on each trip. Paddled by eight or ten men with three-pronged paddles these canoes are a fine sight going out through the heavy surf common on the Ghana coastline; attempts to substitute the canoes with inboard-engined surf-boats have failed because of the difficulty of getting these up the steep beaches—the canoes can easily be 'walked' up because of their rounded line from stem to stern. A mechanization scheme based on outboard motors has, however, been extremely successful, not in reducing the crew number but in increasing the number of trips which can be made in one day and, since under sail the canoes could not get very close to the wind, in giving greater freedom of selection of fishing grounds.

Especially in the francophone ports of West Africa, a number of small fleets of French sardiniers have developed in the last decade; using round-haul nets, these vessels fish mostly for *S. aurita* and *S. eba*, and their catches make up a major part of the *Sardinella* landings of Senegal and the Ivory Coast. About 30 sardiniers operate from the port of Abidjan, for instance, taking around 25×10^3 tons of sardines annually.

There are also *S. aurita* fisheries in the Levant Basin of the eastern Mediterranean Sea, and Rifaat (1960) describes the *Sardinella* fisheries off the Nile Delta during the period before the closure of the Aswan High Dam. During the Nile flood (from August to December) thin, spent sardines moved from the east into the region immediately before the delta. They fed heavily and their fat content increased rapidly, e.g. in *S. aurita*, from 6·4% to 31% of the body weight within this three-month period. After the flood receded and the standing crop of zooplankton diminished the sardines moved away into deeper water. This Egyptian fishery, like that off the coast of Israel, was dominated by *S. aurita* but also included smaller quantities of *S. eba* and *S. granigera*. Now, however, since the closure of the new Nile dam, the annual flood no longer reaches the sea and the fishery appears to have become greatly diminished. In the tropical West African region *S. aurita* is present in small quantities below the thermocline virtually the whole length of the coast (Longhurst, 1964; Williams, 1968). The relation between these small and presumably isolated schools to the populations in the main fishing areas off Senegal, Ivory Coast–Ghana, and Congo–Angola is not known.

S. eba is a deeper and flatter fish than *S. aurita*. It can be found almost everywhere between Mauritania and Angola, except perhaps in the region of the Niger Delta and the Cameroons, where it is replaced by the closely related species *S. cameronensis*, itself also deeper and flatter in form than *S. aurita*. Much less is known of the biology and distribution of these two species than of *S. aurita*. Although they are widely distributed and present everywhere along the coast they are evidently more abundant in the eutrophic regions of Senegal, Ivory Coast–Ghana, and Congo–Angola, where they may at times rival the landings of *S. aurita*; in 1966, for example, nearly 50% of all the landings of the sardine boats from Abidjan were made up of *S. eba* (Marchal, 1967).

S. eba, and presumably also *S. cameronensis*, has a rather catholic diet based upon available zooplankton and to a much greater extent than *S. aurita* the juveniles penetrate into estuaries and lagoons in the same manner as do those of *Ethmalosa fimbriata*. Wherever there are trap fisheries for juvenile *Ethmalosa*, an important component in the catch is contributed by juveniles of *Sardinella eba*, and in the fisheries for adult *Ethmalosa* a certain percentage of adult *Sardinella eba* are normally included in the take; in places where *Ethmalosa* is not abundant, such as the western coast of Nigeria, the rather sparse stocks of *Sardinella cameronesis* form the basis of small fisheries operating either with drift-nets at night, or round-haul nets from large canoes during the day. As with *S. aurita*, both of these species are also taken at some places and at some times of the year in rather large numbers by the big, highly-evolved beach-seines which are such a feature of the West African scene.

In the eastern boundary currents to the north and the south of the tropical area, the fisheries for *Sardinella* are replaced by fisheries for temperate sardines; in the Canary Current this boundary occurs off Mauritania, to the north of which *Sardina pilchardus*, the European sardine, is the main clupeoid fish taken. In the south, the division between the warm-water and the cool-water clupeoid fisheries is around Mossamedes, to the south of which the South African pilchard (or sardine) (*Sardinops ocellata*) is the dominant species. Although not a strictly tropical species, it seems worthwhile to pay some attention to this South African fish both because this occurs off a country with a 'tropical' economy but also because of some interesting features of the results of heavy exploitation of *S. ocellata* which have become evident in recent years. There appear to be two populations of the South African sardine, one centred at Walvis Bay off southwest Africa and the other off St Helena Bay in the Cape Province of South Africa; tagging shows that although there is limited interchange of individuals between these populations, on the whole they are reproductively isolated one from the other (Stander and Le Roux, 1968). In each region the fish appear to concentrate along the boundary between the upwelled Antarctic Intermediate Water of the Benguela Current, and more offshore oceanic water, and it is in this region that there are major fisheries during the winter months when the fish are feeding actively upon the diatom bloom in the upwelled water. Stomach analyses have shown that volumetrically phytoplankton dominates the diet in a ratio of approximately 2 to 1, the phytoplankton utilized being mainly large diatoms, and the zooplankton mainly calanoid copepods. The work of De Jager (1960) and his associates in southern Africa has shown that in summer the stocks disperse from the coastal upwelling areas to spawn offshore; this occurs over a wide region and in two main periods, from August to October, and from January to March. Large fish spawn during the first of these periods and smaller fish during the second. Stander and Le Roux (1968) have recently reviewed the history of the fishery for sardines at Cape Town which began in 1943 and which has recently shown indications of serious problems (Table I). The catching capacity of the purse seine fleet has continued to increase from a total hold capacity of $4{\cdot}8 \times 10^3$ tons in 1950 to $11{\cdot}7 \times 10^3$ tons in 1965, yet the catch has in recent years began to decline from peak landings of more than 400×10^3 tons in the years of 1962 and 1963. There have been considerable fluctuations in the percentage of individuals smaller than the length at which first maturity is reached, from year to year; this is due to variation in recruitment of the various year classes and the success of spawning; however, there has been a tendency since the mid-1950s for the percentage of juveniles in the landings to rise from values of less than 10% to above 50% in recent years. A general trend towards a decline in population size as a result of a failure of a number of year-classes to provide sufficient recruits led to a very sharp reduction in pilchard landings subsequent to 1963. By 1969 (Stander, pers. comm.) the fishery for *Sardinops* at Cape Town was reduced to only 50×10^3 tons or about one-eighth of its peak production, while about 250×10^3 tons of anchovy were taken. In 1963 abnormally high water temperatures, more than 4° C higher than usual, off the coast of South West Africa, especially in May and June apparently caused a complete spawning failure and the decline in the pilchard fishery was consequently accelerated by the complete recruitment failure of the 1963 year-class. The catch from the northern population of *Sardinops* off southwest Africa continues higher, however, than that off Cape Town, with a quota in 1969 of $1{\cdot}0 \times 10^6$ tons for land-based processing and $0{\cdot}57 \times 10^6$ tons for floating processing plants. There are indications, again, of falling catches and in 1969 the plants at Luderitz did not fulfil their quotas, and 250×10^3 tons of anchovies were processed. The apparent decline in the stock of pilchards is evident not only in commercial landings but also in the number of eggs taken in egg and larva surveys by research vessels, and in the catch rate of adults sampled by blanket-nets from research vessels during the same period.

TABLE I

Statistics of the South African fishery for Sardinops ocellata *at Cape Town (adopted from Stander and Le Roux, 1968); weights in short tons.*

Year	Number of boats	Total hold capacity of fleet	Tons, total landings	Tons per hold capacity	Juveniles in catch %	Juvenile anchovies in research ship catches %	Anchovy commercial landings
1950	150	4,850	95,093	10·50	7·31	—	—
1951	183	6,400	109,610	12·01	2·89	—	—
1952	197	7,260	187,424	22·23	12·31	—	—
1953	229	8,320	150,987	15·73	3·11	—	—
1954	225	8,470	97,336	11·07	0·92	—	—
1955	228	8,300	134,424	13·55	0·07	6	—
1956	222	8,210	84,156	8·02	6·29	8	—
1957	210	8,210	118,557	9·41	15·86	33	—
1958	201	8,480	214,528	22·15	53·15	34	—
1959	165	8,660	286,796	30·90	64·65	81	—
1960	143	8,310	350,361	42·16	51·86	38	—
1961	131	9,310	443,449	47·64	15·57	60	—
1962	122	9,840	452,735	46·01	30·62	0	—
1963	127	10,920	441,943	40·47	52·69	96	23
1964	126	11,350	282,301	24·87	52·55	89	95
1965	125	11,730	222,920	19·00	52·63		209

The South African pilchard shares its environment with an anchovy (*Engraulis capensis*) which apparently has a very similar ecology; the distributional ranges, and the diet of the two species overlap very strikingly (Stander and Le Roux, 1968). and it may be presumed that in some way the populations of the two are in a dynamic balance so that their combined biomass equals what can be supported by the planktonic food-chain. Both include a small number of copepod species in the dominant components of their diet (*Calanoides carinatus*, *Centropages branchiatus*) and a number of diatoms are similarly common to the diet of each (*Nitzschia*, *Thalassiosira*, *Skeletonema*, *Chaetoceros*). There is some evidence that the stock of *Engraulis* has increased as that of the pilchard has decreased at Cape Town; in the routine blanket-net catches from South African research vessels the ratio of anchovies to pilchards has changed (Table I) from approximately one anchovy to 15 pilchards in the mid-1950s to more than 10 anchovies for each pilchard taken in the mid-1960s; this led to the initiation of an anchovy fishery in 1963 out of Cape Town, which at first had limited success but now appears to be established. We shall meet similar examples of competition between sardine-anchovy species-pairs in the Indo-Pacific in considering the Californian and other fisheries.

WESTERN ATLANTIC

In the enormous warm-water area of the western Atlantic, which extends effectively from New England to Argentina, there is a less distinct division between tropical regions and the warmer parts of the western boundary currents than in the eastern Atlantic; in this whole area there are approximately 75 species of clupeoids—considerably more than in the eastern Atlantic. Of these, some dozen or so are significantly utilized in the warm-water fisheries.

The species which are exploited range from such small and relatively unimportant forms as the little anchovy, *Anchovia clupeoides*, which is common in the fish markets of the Caribbean and Brazil, to the very important fisheries for menhaden (*Brevoortia* spp.), which occur in relatively low latitudes and, although strictly outside the tropical area are so similar to the West African *Ethmalosa* fisheries as to be of interest to us here. There are no major fisheries in the western tropical Atlantic which depend upon anchovies of the family Engraulidae; there are, however, a number of local fisheries, similar to that for *Anchovia clupeoides* mentioned above, for rather less than a dozen species of anchovies. Among these are the bay anchovy (*Anchoa mitchilli*) which occurs from Cape Cod to Yucatan and is an inshore species, feeding on small zooplankton and having some commercial use in the manufacture of anchovy paste in the southern United States. *A. hepsetus* occurs from Chesapeake Bay through the tropical region to Uruguay and migrates along the eastern seaboard of North America in the summer where some $10–15 \times 10^3$ tons are taken annually; it is also abundant in the West Indies where it is the object of a number of small fisheries. On the eastern seaboard of South America *A. tricolor* occurs from Venezuela to Argentina, and is commonly found in fish markets throughout this region. About 13 species of the genus *Anchoviella* occur in the western tropical Atlantic and, of these, two (*Anchoa perfasciata* and *A. elongata*) are fished to some extent in Central America and the Caribbean. The freshwater anchovies, *Pterengraulis atherinoides*, and several species of the genus *Lycengraulis* are important in inland fish markets of the Amazon Basin through to Venezuela. The major clupeoid fisheries of this area are based upon the Clupeidae. Leaving aside the fisheries for the Atlantic and Gulf shads, *Alosa sapidissima* and *A. alabamae*, and that for the river herring, *Pomolobus chrysochloris*, we find that there are two major fisheries for clupeoids to be considered: that for menhaden (*Brevoortia*) in the Gulf of Mexico and on the Atlantic seaboard of the United States and also off the southeastern coast of South America, and that for *Sardinella* off Venezuela and Brazil.

Two species of *Sardinella* appear to be important along the tropical eastern coast of South America; these are *S. anchovia* along the coast of Venezuela and *S. brasiliensis* which appears to replace it in the region of the Guianas. There has been considerable confusion in the literature as to the nomenclature of these species and both have on occasion been referred to as *S. aurita*, but it is doubtful whether they are conspecific with the West African species; *S. anchovia* also frequently appears in the fisheries literature under the name *Clupanodon pseudohispanica.* The major population of *Sardinella anchovia* is concentrated along the eastern coast of Venezuela between Margareta Island and the Gulf of Cariaco. The recent work of Simpson and Gonzales (1967), and Simpson and Griffiths (1967) have provided much information about this important species, which has produced landings generally fluctuating from 30 to 40×10^3 tons annually in the last decade, and reaching a high level of 44×10^3 tons in 1965. The life history of *S. anchovia* is very closely tied to the upwelling cycle in the eastern region of Venezuela. The fishery is mostly concentrated in the Gulf of Cariaco and it is this population which has been most studied; it is quite likely that other populations in more open sea regions have parallel relationships with local upwelling cycles. The Gulf of Cariaco is an east-west trending gulf, long and narrow with a relatively narrow entrance almost closed by a sill at 60 m depth. During the non-upwelling part of the year, water in the Gulf at depths greater than the sill depth are not replaced and frequently become anaerobic. The northeast trades reach their peak strength between December and April and during this time they displace much surface water from the Gulf which is replaced by an undercurrent across the sill; this replacement water upwells over much of the area of the Gulf and the resultant eutrophication and high standing crop of plankton coincides with the spawning peak of the Gulf population of *S. anchovia* (Simpson and Gonzales, 1967). At present the fishery is based almost entirely upon beach-seines which are extremely efficient and whose operation is frequently arranged so as to capture complete schools of fish. The maximum weight of these schools appears to be in the region of 400 tons but 60% of them contain less than 100 tons of fish and 90% of them contain less than 20 tons of fish. Although this beach-seine fishery is extremely efficient so far, there is no evident reduction in the catch/unit effort of this fishery. It has been possible to age *S. anchovia* by a study of scale annuli, and the age composition of the catch appears to be weighted heavily in favour of 2- and 3-year old fish which together comprise more than 70% of the total landings (Heald and Griffiths, 1967). First year fish of about 14 cm in total length are not fully recruited to the beach-seine fishery. This fishery also takes small numbers of *S. brasiliensis* which are at the extreme northern limit of their range in eastern Venezuela and can readily be distinguished from the more usual species by their deeper bodies.

There are similar but considerably smaller fisheries for the anchovy *Cetengraulis edentulus* on the Peninsula of Araya, during the wet season from May to November when the sardine fishery is less active, and up to 5 thousand tons of anchovies may be taken which are used for the production of fish meal. The thread herring *Opisthonema oglinum* is taken in similar quantities in a number of localities scattered along the coast by small beach-seine fisheries, but is nowhere very important. The future of clupeoid fisheries in this region, considering the rather wide area over which strong seasonal upwelling occurs and which coincides with the distribution of *Sardinella anchovia* (ascertained by egg and larva surveys), appears to be promising. It is likely that the beach-seine fishery will be supplemented by a normal boat purse-seine fishery offshore since according to Simpson *S. anchovia* may, at present, only be exploited at the extreme periphery of its range; however, operations of U.S. fishery research vessels off the Venezuelan coast have not indicated abundant offshore stocks of *Sardinella* (Bullis and Thompson, 1968).

Further to the south, along the coast of Brazil, there is a fishery for *S. brasiliensis* in the southern part of that country between Santos and Rio de Janeiro. The age composition in these two places is known and it is evident that the stock of *S. brasiliensis* includes a much greater number of year-classes than does the population of *S. anchovia* in more tropical areas. At Rio de Janeiro, seven year classes may be detected in the population, but at Santos only three. It also appears that the Santos stock contains no mature individuals, but only juveniles and fish in the early stages of maturation; at Rio de Janeiro the stock includes all stages of maturity. It is not clear whether this indicates long migrations of the population, which would not be impossible, or whether the fishery is taking only the edges of two improperly understood stock distributions. On the face of it, perhaps the second interpretation seems more likely.

Seven species of *Brevoortia* are distributed in the western Atlantic. Of these, five occur in the Gulf of Mexico and along the Atlantic coast of North America, while two occur on the coast of South America. Of the five North American species, two (*B. tyrannus*, the Atlantic menhaden, and *B. patronus*, the Gulf menhaden) form the object of one of the major fisheries of the world and together yielded a yearly catch in excess of 1×10^6 tons in the early 1960s. Minor catches are made of the yellowfin menhaden, *B. smithii*, and the finescale menhaden, *B. gunteri*, the former off Florida, and the latter on the northern coast of the Gulf of Mexico. *Brevoortia* has an ecology extremely similar to that already described for *Ethmalosa fimbriata* in the Gulf of Guinea. All species appear to have a very fine filter basket formed of gill rakers and their food appears to be dominated, at least where they are available, by larger members of the phytoplankton community; it is supposed that the long seasonal migrations which the species undertakes are arranged to carry them into areas of diatom and dinoflagellate blooms. When not in such areas, their food consists of microzooplankton. Spawning occurs rather early in the year and the eggs are hatched in offshore waters; this may be as early as January and February in the southern part of their range on the western coast of Florida but further to the north during spring and early summer. After some weeks growth, at about 1 inch in length, the larvae enter estuaries where they spend the rest of the summer (June, 1959, 1960), leaving them only at the onset of cold weather; while in the estuaries the juveniles form typical clupeoid schools and undergo much predation from fish-eating birds. Their dominant food during this period comprises estuarine diatoms. After spawning, the adult stocks move northward along the Atlantic coast from their rather deep wintering grounds off Florida and westward along the north coast of the Gulf of Mexico from the same general wintering area. The migration takes place in the upper mixed layer where they are extremely vulnerable to spotting from masthead lookouts or light aircraft, and are readily taken with large purse seines.

The Atlantic fishery, based upon *Brevoortia tyrannus*, started to decline from peak landings in 1956 when, to some extent, the fishing vessels either changed to other fisheries in the same region or shifted their effort into the Gulf of Mexico on to *B. patronus*. The last important year-class of *B. tyrannus* was that of 1958, which remained in the fishery and resulted in excellent catches until the year 1962 (Table II); since then production has declined.

TABLE II

Recent landings of menhaden in the western Atlantic: metric tons × 10^3.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
					Brevoortia tyrannus + B. patronus					
United States Atlantic coast	658·1	550·4	587·0	585·7	384·7	302·0	318·9	233·6	210·2	251·3
Gulf	341·0	381·4	462·9	479·3	438·9	410·1	464·0	359·7	317·6	375·0
					Brevoortia pectinata + B. aurea					
Brazil			3·0	1·2	1·3	1·4	1·1	1·6	1·2	—

Off South America, southern Brazil, Uruguay and northern Argentina, there are small fisheries for *B. pectinata* and *B. aurea*, but they do not approach by an order of magnitude the importance of the North American *Brevoortia* fisheries. At Valparaiso, *B. pectinata* are taken to be salted or smoked for human consumption as are *Ethmalosa* in West Africa, while in North America the *Brevoortia* landings are used entirely for industrial purposes.

EASTERN PACIFIC

On the western side of the American continent the warm water of the Pacific Ocean, as in the eastern tropical Atlantic, spans a relatively small range of latitude. It appears that approximately 25 species of clupeoids occur abundantly. Numerically, these are dominated by 11 species of the genus *Anchoa* (several of which were considered as *Anchovia* by Meek); these are small, mostly zooplankton-feeding species, although *Anchoa starksi*, which occurs from El Salvador to Ecuador is also recorded as including abundant diatoms in its diet. Some species have rather wide distributions, occurring throughout the tropical region, as, for instance, *A. naso* present from the tip of Baja California south to Peru; but several are rather restricted, for example *A. eigenmannia*, which occurs only between Costa Rica and Panama.

The trawl fisheries for shrimp in the Gulf of Panama and elsewhere along the western coast of Central America catch many species of clupeoid fish as a by-product; Peterson (1956) indicates the diversity of this fauna in which *Ilisha*-like fish are prominent. Local fisheries for a number of species, particularly of the genus *Anchovia*, supply the fish markets in coastal towns the length of the tropical coast. Recently, small-scale reduction plants have been established in Panama and Ecuador and are partly supplied by trash-fish, mainly clupeoids, from the shrimp fisheries, and partly by specialized fisheries—as in the Gulf of Panama—for the tropical anchoveta, *Cetengraulis mysticetus*, and for the thread herring *Opisthonema libertate*. The Panama fishery reached 65×10^3 tons in 1968, of which 12×10^3 were of thread herring, the remainder of anchoveta (Gulland, 1969).

Tuna boats, both of United States and Central American origin, for many years relied almost entirely upon *Cetengraulis mysticetus* for the live bait essential for their tuna fishing operations; as Peterson (1956) has indicated, one of the main fisheries for this species was in the Gulf of Nicoya and between 1939 and 1951 this species was virtually 'fished out' from this Gulf. Although it is possible that its disappearance (as indicated by the figures given in Table III) could have been the result of climatic changes, it is probably that the species was simply reduced below its survival point by the activities of the tuna bait-boats: it has subsequently been re-introduced successfully by the same boats back into the Gulf of Nicoya. *C. mysticetus* has a diet in which phytoplankton is extremely important; as Bayliff (1963) shows, the stomach is muscular and gizzard-like, a character it shares with other phytophagous clupeoids and with mullets. Centric diatoms such as *Coscinodiscus* form a

TABLE III

Statistics of the tuna bait-boat fishery for Cetengraulis mysticetus *in the Gulf of Nicoya.*

Year	Total catch (scoops $\times 10^3$)	Mean catch rate (scoops/day)
1939	220·7	454
1940	25·3	186
1941	89·6	199
1942	19·2	258
1943	54·7	471
1944	23·5	165
1945	29·3	126
1946	90·2	279
1947	57·5	92
1948	7·1	44
1949	1·2	59
1950	—	0
1951	—	0

dominant part of the diet of young fish; adults tend, on the other hand, to feed on benthic diatoms such as *Melosira*, and Bayliff demonstrated that their stomach contents correspond well with the benthic diatom flora of their habitat. The population of *Cetengraulis mysticetus* in the Gulf of Panama has been studied by Howard and Landa (1958) who showed how rapidly its stock was turned over by reproduction and mortality. They found that although there was some spawning throughout the year this was at peak intensity in November and December and coincident with the annual period of upwelling. Bayliff showed that the size of first year fish and their abundance could be related to the strength of upwelling and population densities of adults. Reproduction occurs at the end of the first year of life when the fish have reached approximately 13 mm in length; in the second year, little more than another centimetre is added to the length of the fish, which this year reach maturity earlier than the yearlings and have an overall longer spawning season. The total population as sampled by the fishery may be comprised of more than 90% of first-year individuals (Table IV); this type of population structure appears to be typical of tropical clupeoid fish.

The eastern boundary currents which flow towards the tropical regions from the north and the south in the eastern Pacific Ocean each contain a pair of species, one sardine and one anchovy, which are the dominant clupeoids; in the south, off Peru and Chile, the anchovy is dominant and occurs in very great abundance, while in the north, in the California Current, the sardine was dominant until suppressed by fishing pressure, assisted by climatic changes which were in favour of the anchovy; at present, therefore, anchovies are dominant in both the Peru and California Currents. The eastern boundary current off Peru and Chile supports the largest single-species fishery in the world, and approximately 20% of all the world's landings of sea fish are taken by this fishery; this may be attributed to three factors, (1) the great quantity and high rate of carbon fixation by phytoplankton in the Peru Current, (2) the phytophagous habit of the anchovies concerned and hence the extremely abbreviated nature of the food chain, and (3) a relatively very high growth rate. Upwelling in the Peru Current is extremely strong and occurs for about 270 days each year over an area of about $0{\cdot}5 \times 10^6$ km^2

TABLE IV

Percentage age composition of catches of Cetengraulis mysticetus *at a number of Central American locations (Barrett and Howard, 1961).*

Location	Year class I	II	III
Guaymas	77·7	22·3	—
Ahome	81·4	18·6	—
Banderas	83·8	16·2	—
Fonseca	33·5	54·5	12·0
Columbia	41·4	58·6	—
Ecuador/Peru	90·1	7·8	2·1

(Cushing, 1968) at an average rate of 3×10^{12} cm³/sec (Wyrtki, 1966). As Cushing shows, about 155×10^6 tons of carbon may be fixed annually, a figure only exceeded for other coastal upwellings by that of the Benguela Current with 278×10^6 tons.

The anchovy (*Engraulis ringens*) of this region is very similar in general form to other members of the genus but is particularly distinguished by the occurrence of rather fine filaments on the gill rakers; these occur early in life compared with similar species elsewhere. This is related to the ecology of the species, whose diet is based upon phytoplankton, primarily diatoms, to a considerably greater extent than any other species of *Engraulis*. Investigations of *E. japonicus* and *E. anchoita* indicate that the diet of these widely separated species, one off Japan and one off Argentina, is rather similar; zooplankton dominates until the fish are 15 or 20 mm in length, after which phytoplankton becomes increasingly important in the diet, though apparently not to the same extent as in *E. ringens* off Peru. It is to be expected, however, that even this latter species in its early larvae stages will depend largely upon microzooplankton for its food.

Although it had been known for very many decades that theres was a large stock of *Engraulis* off the coast of Chile and Peru, it was not until 1940 that an industrial fishery was attempted; to a certain extent the reluctance to begin fishing this species was based on the supposition that the economy of the very important guano-producing birds of the Chile and Peru Currents depended upon the anchovy. It was supposed that the population of these birds was limited by food, even though in retrospect it is evident that the successful attempts of the guano administration of Peru to increase the population size of the guanay cormorants and of pelicans by statutory protection of the breeding populations and by increasing their available nesting sights by

TABLE V

Growth statistics of the Peruvian fishery for Engraulis ringens: *data derived from several sources.*

	Number of fishing boats	Number of reduction plants	Total landings (tons × 10^6)	Fish meal production (tons × 10^6)
1955	175	16	0·059	0·021
1956	220	27	0·119	0·031
1957	272	39	0·326	0·064
1958	321	53	0·737	0·121
1959	355	63	1·909	0·323
1960	654	89	2·944	0·553
1961	753	105	4·580	0·864
1962	1,090	120	6·275	1·120
1963	1,756	150	6·423	1·129
1964	1,836	155	8·863	1·548
1965	1,654	148	7·233	1·282
1966	1,670	144	8·530	1·466
1967	1,350	151	9·825	1·804
1968	1,172	120	10·263	1·922
1969	1,308	112	8·850	1·611

artificial means, indicate that the limiting factor for population size of these birds was not the amount of food available but rather nesting site limitation. As the tabulated data show, the commercial fishery which began in the early 1950s after an initial period of establishment grew very rapidly and soon placed Peru among the major fishing nations of the world. From landings of a few tens of thousands of tons in the mid-1950s, they had climbed in 10 years to more than 8 million tons per annum (Table V), while the number of boats and of reducing plants had increased in the same period by approximately an order of magnitude. The effect of this industrial expansion upon the economy of an underdeveloped country such as Peru has been very important. Throughout this period of expansion there has been a considerable amount of apprehension on the part of industrialists and biologists associated with the fishery as to the possible effect on it of the occurrence of El Niño conditions; during these incursions into the updwelling region of a layer of warm surface water the anchovies occur deeper than usual, remaining in the colder sub-thermocline water where they are unavailable to the populations of fish-eating birds; cormorants and pelicans are thus unable to dive far enough to catch fish successfully and emigrate and starve in very great numbers; the population dropped, during the last recorded severe El Niño, from about 16 million birds to perhaps 3 or 4 million birds. It was supposed that the reaction of the anchovies to El Niño conditions might have similar effects upon the success of the small bolicheros or purse-seiners used by the Peruvian fishery and this remained a spectre hanging over the development of this industry since it has been found that the seiners could not reach deeply enough to take fish under these conditions.

Recent studies on the population biology of the Peruvian anchovy show that the species occurs from northern Peru to central Chile, and seasonally further to the south, and that on the basis of meristic counts (Brandhorst, Careno and Rojos, 1965) at least three stocks occur, two off Chile and one off Peru; it is important to determine the degree to which the Peruvian stock, upon which most of the fishery is based, is independent of the southern stocks (Schaefer, 1967). Spawning occurs throughout the year south of Punta Aguja at 6° S, although two spawning peaks occur, one in October and the other, less important, in February or March; the young fish spawned in October begin to appear in the fishery as early as the end of the summer, while the young fish from the second spawning peak are recruited the following spring in July to September (Saetersdal and Valdivia, 1964). Recruitment to the fishery begins, early in the year, at 8 cm when the fish (at this time called peladilla) are about 5 months old, and is virtually complete in October at about 14 cms (Saetersdal and Valdivia, 1964); but, as Gulland (1969) points out, the time of greatest availability to the fishery does not correspond with expectation. In the period June–September when two year-classes are present in the fishery, apparent abundance is actually least, probably because of spawning-related behaviour of the fish and perhaps because the population has been heavily fished. Growth has been determined principally by the Petersen method, (Saetersdal and Valdivia, 1964) which gives good results only up to an age of 18 months; but from otolith studies Boerema et al. (1965) demonstrate that few fish survive beyond the second year of life. Growth is very similar to that of the tropical anchoveta *Cetengraulis mysticetus* discussed above, and a fork length of 13 cm is reached at the end of the first year of life. Growth can be approximated to the von Bertalanffy equation which has constants of $k = 1{\cdot}7$ and $L_\infty = 15$ cm.

As Schaefer (1967) discusses in his review, the age structure of the exploited population appears to be getting younger and though, as he points out, it is difficult to identify year-class variation during the decade of the fishery, such variations between 1961 and 1966 appear to be rather small, and vary by a factor of less than 2·0; in high-latitude clupeoids, such as the North Atlantic herring *Clupea harengus*, year-class strength may vary by a factor more than 10 times greater.

Schaefer uses as a unit of effort the catch per boat/ton/month to estimate the stock abundance of anchovies off Peru, and from his regression of effort on catch per unit effort obtains an estimate of the maximum sustainable yield of between $7{\cdot}7 \times 10^6$ metric tons per annum and $8{\cdot}1 \times 10^6$ metric tons per annum, depending on whether or not the calculations are corrected by a factor for increasing vessel efficiency during the period. He notes that the yields for the seasons 1964–65 and 1965–66 were very close to the maximum sustainable yield, and in fact may have exceeded it slightly. He, therefore, deduces that the fishery has now reached a point at which regulation is obviously essential to its continuing well being. It can also be estimated from a knowledge of the daily food intake of guano birds that the total stock of fish-eating birds on the coast of Peru consumes approximately 2·5 million tons per year and this, added to the sustainable yield estimate derived from the fishery, suggests that the total yield from the anchovy population could be in the order of 10 million tons if the birds were eliminated. Schaefer suggests that a minimal population of 3 million birds may be essential for their survival for the future in case the guano industry again became of greater importance than the fish meal industry; he bases his calculations on the population size at the time of reduction by El Niño; whether or not this is desirable is a matter for Peruvian economists to determine. Also, as Gulland (1969) points out, the relationship between anchovy stock size and the numbers of guano birds is probably rather complex. Although it was the case in the past it is not certain that the bird population is now size-limited by nesting sites. Although a careful study does not seem to have been made, there are indications that the bird populations are not recovering as fast from the most recent El Niño-related population collapse as they have in the past.

The great fishery for *Engraulis ringens* off Peru and northern Chile and the overwhelming dominance of this species in the pelagic ecosystem draws attention to the fact that in this region we again find an anchovy-sardine species pair. The sardine of the southeast Pacific Ocean, *Sardinops sagax*, forms the basis of a small fishery off northern Chile, where some 10×10^3 tons are taken annually; two species of *Ethmidium*, locally known as machete and machueol, give catches of about 20×10^3 tons in southern Peru. It would be extremely interesting to obtain historical data on the relative abundance of sardines and anchovies in the Chile–Peru region comparable with data from the sub-fossil record of California discussed below.

The clupeoid fisheries off California are of interest to us here even though they are prosecuted in mid-latitudes rather than in the tropics, because they are again based on a pair of species—one anchovy and one sardine—which have been studied in great detail and which show some interesting changes in relative abundance because of an intensive fishery on only one of them, the California sardine. *Sardinops caerulea* of California is extremely similar to, and may be conspecific with, the Peruvian-Chilean species, while the California anchovy, *Engraulis mordax*, is distinguishable from the Peruvian anchovy principally by the number and length of its gill rakers which are fewer, shorter, and less well adapted to a diet based primarily upon phytoplankton. The growth rate and population structure of both these species is quite different from the Peruvian species; both grow considerably more slowly so that their populations include a greater number of year classes. While few individuals of *E. ringens* off Peru survive beyond 18 months of age, fish of 5–6 years old form a significant part of the population of *E. mordax* off California.

Briefly, the history of the decline of the sardine fishery of California is as follows: from its start, in the early part of the century, the fishery rose to a peak of sardine landings in the early 1940s; these then progressively declined

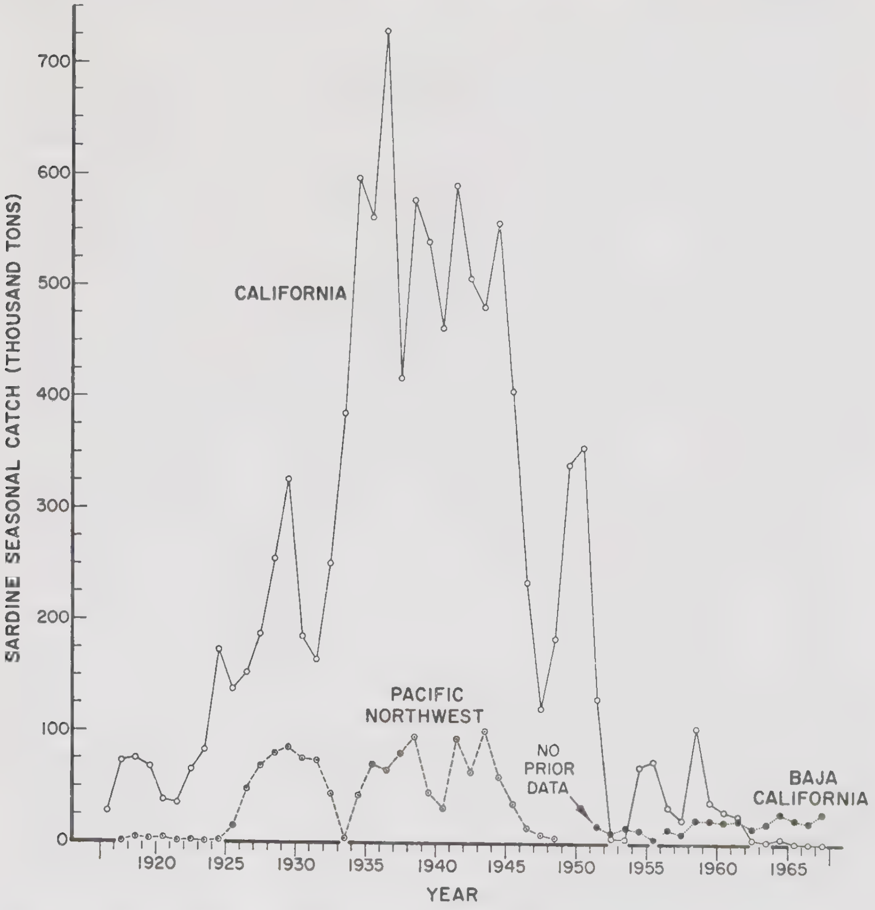

Fig. 1.—Annual catches in the fishery for Pacific sardine (*Sardinops caerulea*) in Oregon-Washington, California and Baja California, 1915 to present day (redrawn from Ahlstrom, unpubl.).

and with the exception of a minor resurgence in the late 1950s, continued until the present situation was reached (Fig. 1, Table VI). The fishery is now so small as to be negligible and a complete moratorium may be imposed on the fishing of this species off the State of California; this decline from landings of more than half-a-million tons in the early 1940s to a few hundreds of tons in the mid-1960s has had important economic effects upon the California fishing industry. Continuing egg and larval surveys in the California Current have confirmed that the decline in the landings has been a result of a declining total population of the northern race of the species which has now almost disappeared; the only remaining populations of any fisheries significance are isolated stocks in the Gulf of California and along the southern part of the west coast of the Baja California peninsula. As the stock of sardines declined, as indicated both by the catches of the fishing fleet and the findings of the egg and larval surveys (Fig. 2), so these latter indicated that the biomass of anchovies in the same region was increasing. By the mid-1960s it had become evident from these data that the biomass of anchovies had risen to such an extent that it had essentially replaced the original sardine biomass which had been present at the height of the fishery in the 1940s.

The reasons for the decline in the sardine fishery and the rise in the anchovy stock are certainly complicated but some very reasonable explanations which are probably near the truth have been put forward by Marr, Murphy and others. The models recognize certain basic ecological differences between the anchovy and the sardine in an environment unaffected by the fishery. The area over which the anchovy spawned in the early 1950s and presumably that over which it was generally distributed was more restricted than the spawning distribution of the sardine since the anchovy eggs and larvae occurred primarily along the coast, especially in certain regions in which there is strong and regular upwelling. The fecundity of anchovies, weight-for-weight, appears to be about twice that of the sardine and (perhaps more important) the year-class variation of the anchovy, as off Peru, appears to be much smaller than that of the sardine. The feeding ecology of the two species in the California Current, including that of their larvae, appears to be rather similar and it is likely that the two species are in competition for food, so that their total combined biomass, as Lasker (1970) has suggested, is probably food dependent and is thus limited by the total zooplankton production of the California Current. Finally, in general the anchovy appears to be a more northern species, its lower temperature limit for spawning being 2° C lower than that for the sardine. Anchovies spawn in water warmer than 11° C, while sardines spawn only at temperatures greater than 13° C. Two factors perhaps explain the decline of the sardine population and the rise of the anchovies; these are; first, the selective fishing pressure on the sardine, which was heavily sought by a fishery that almost neglected the anchovy; and, secondly, the beginning of the major decline in sardine stocks coincided with the start of an anomalous period in the California Current, from 1943 to 1957, of unusually cold conditions and of unusually strong and regular upwelling. These conditions might be expected to favour the anchovy at the expense of the sardine and to make it unlikely that abundant year-classes of the sardine would occur during this period; in fact, the only major year-class during this period resulted in a minor resurgence of the fishery during the late 1950s. The degree to which an increasing biomass of the anchovy

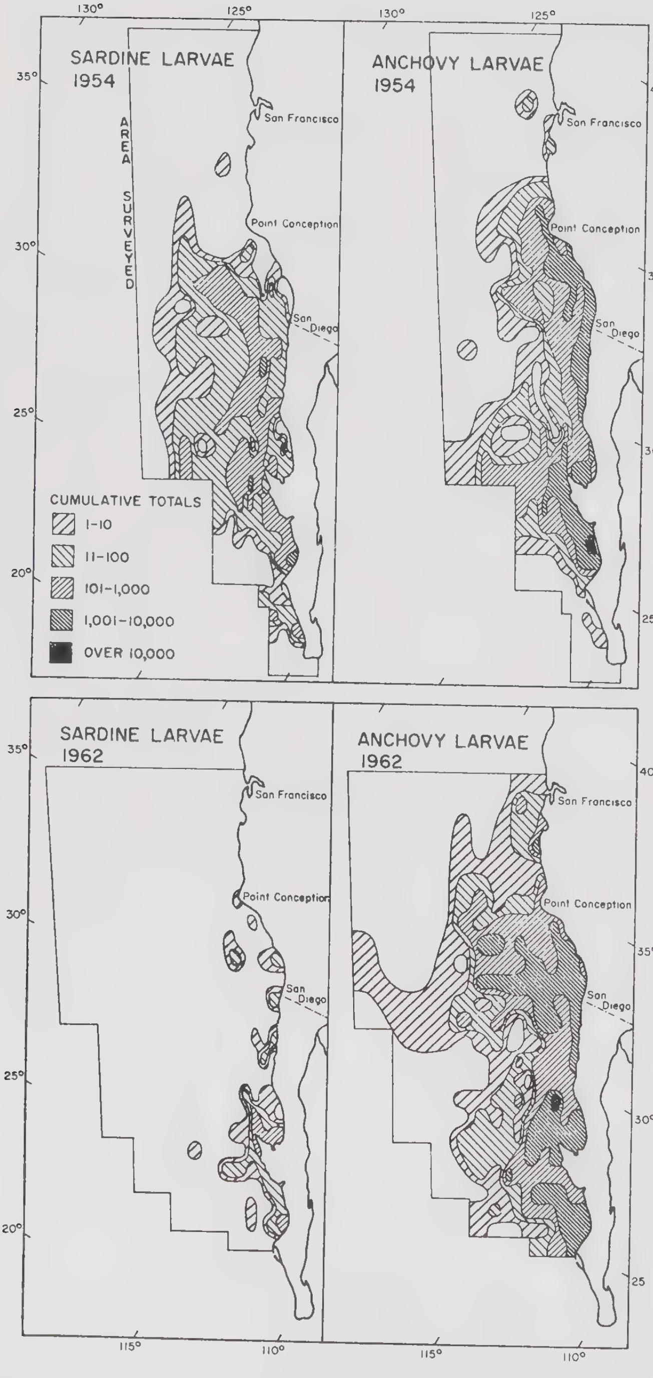
SARDINE LARVAE 1954
ANCHOVY LARVAE 1954
SARDINE LARVAE 1962
ANCHOVY LARVAE 1962
AREA SURVEYED
San Francisco
Point Conception
San Diego
CUMULATIVE TOTALS
1-10
11-100
101-1,000
1,001-10,000
OVER 10,000
130°
125°
115°
110°
35°
30°
25°
20°
40°

Fig. 2.—Relative abundance of sardine and anchovy larvae in ichthyoplankton surveys of the California Current in 1954 and in 1962 (Cal COFI data).

population has contributed directly, by competition, to the decline of the sardine stocks is not clear, and it is now generally supposed that the anchovies increased in number in response to the ecological vacuum left by the decline of the sardine, rather than that the sardines declined because the anchovies had become so abundant; this is indicated both by a lag in the biomass response of the anchovy to the decline of the sardine (Murphy, 1966) and also by failure to demonstrate decreased survival success as indicated by larval length-frequency distribution of sardine larvae by many thousands of plankton samples in which sardine larvae occurred alone, anchovy larvae occurred alone, or the two occurred together (Isaacs, 1965); however, Gulland (in prep.) has suggested that a relationship exists between the survival of sardines to recruitment and the total spawning biomass of sardines and anchovies.

There is also historical evidence (Soutar, 1969) from the occurrence of scales of anchovies, sardines, and other pelagic species in the varved mud sediments of several of the anaerobic basins in the Santa Barbara Channel that similar shifts in biomass dominance cold water species associated with the anchovy, and warm water species associated with the sardine, together

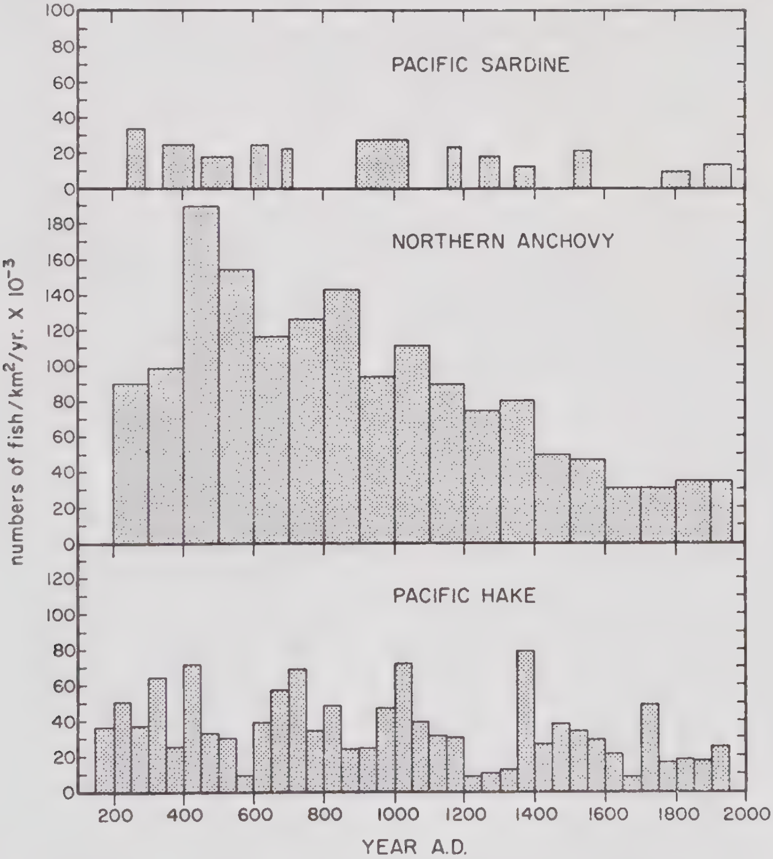

FIG. 3.—Abundance of hake, anchovy and sardine in the California Current at 34° N, as deduced from sub-fossil fish scales in varved deposits in the anaërobic Santa Barbara Basin (redrawn from Soutar, 1969).

with the two main species, had alternated during the many thousands of years during which the varved sediments were being deposited (Fig. 3). It seems very likely that this will prove to be a general phenomenon in such fisheries and the mechanics of the situation must certainly be understood; in particular, it is very important to be able to predict whether the situation is reversible, so that by proper management sardine stocks can be brought back in an area to replace those of the less valuable anchovies. It is unfortunate for the fisheries concerned that the less valuable species appears, from its ecology, to be likely to provide the basis of a more stable fishery than one based on the more valuable species; however, as Gulland (1969) suggests, the potential yield of the two-species system may be greater when it is in the anchovy phase. From the historical data, the potential yield of the sardine in the California Current was evidently considerably less than $1{\cdot}0 \times 10^6$ tons but it seems probable that a sustained yield of up to $2{\cdot}0 \times 10^6$ tons of anchovies may be achieved. A total spawning biomass of up to $4{\cdot}0 \times 10^6$ tons is indicated by egg and larval surveys in the mid-1960s, and from values for the natural mortality rate derived from the age structure of the population Gulland suggests that about half the biomass can be removed annually.

INDO-PACIFIC

The central and western Indo-Pacific region encompasses a very large part of the tropical oceans stretching from the Red Sea to Madagascar, from the Chinese coast to Indonesia and Australia, and through the island archipelagos of the Pacific Ocean; this vast region contains a very great variety of ecological situations ranging from intense upwelling area off the desert coasts of the northwest Arabian Sea, through the oligotrophic oceanic regions of the central Pacific to the rich, shallow, brackish areas of the Indonesian archipelago where estuarine and mangrove conditions occur over very large areas. The Indo-Pacific region also contains the greatest number and diversity of species of clupeoids in the tropical oceans; along the mainland of Asia from China to the Red Sea, down the coast of eastern Africa, and through the Indonesian, the Philippine, and the Australian archipelagos the systematic diversity of clupeoids is baffling to the non-specialist: there are at least 11 species of *Sardinella*; rather similar to these are 15 or 16 species of *Harengula*, and a half-dozen species of *Clupeoides*; there are at least a dozen species of *Ilisha*, or forms very close to this genus, and the little fresh and brackish water herrings of the family Pellonulidae are represented by many genera and species; entering the rivers are a number of important shad-like clupeoids dominated by three species of *Hilsa*, and three species of the very similar genus *Macrura*; round herrings of the genera *Spratelloides* and *Dussumeria* are important and represented by several species each, as are gizzard shads of the genera *Dorosoma* and *Nematalosa*. Anchovies are represented perhaps most importantly by several species of the genus *Stolephorus*, but also by several *Setipinna*, *Lycothrissa*, *Coilia*, and *Thrissocles*.

CENTRAL PACIFIC

In the central Pacific region there appear to be no major clupeoid resources, since the main upwelling feature in this region, the divergence zone extending along the equator almost the whole width of the Pacific Ocean does not appear to support big stocks of clupeoids, but is exploited by other groups of oceanic fish. At Hawaii, the only clupeoid resource of any consequence is an engraulid, the nehu (*Stolephorus purpurpus*) and this is mainly of importance as bait-fish for the live-bait boats of the skipjack fishery; live-bait is frequently in short supply and attempts have been made to substitute other species, even to the extent of the pond-rearing of African cichlid fishes for use on the bait-boats; Murphy (1966) describes the introduction of *Harengula vittata* from the Marquesas Islands to the Hawaiian archipelago, and although this appears to have been successful it has not solved the problem of the lack of live-bait. In most of the oceanic archipelagos and around oceanic atolls, shoals of clupeoids are abundant and many small anchovy-like genera in particular are familiar and important members of the fish fauna around coral reefs, but nowhere are these resources present in massive enough abundance to support important fisheries. It is, in fact, curious that these large shoals of anchovy-like forms are supported by the plankton production around oceanic reefs; the clarity of the water and the lack of phytoplankton blooms seems at odds with the occurrence of relatively abundant shoaling clupeoids.

WESTERN INDO-PACIFIC

Probably the most important clupeoid fishery of the western Indo-Pacific at the present time is that for the Indian oil sardine (*Sardinella longiceps*). Stocks of this species extend around the whole perimeter of the northern part of the Indian Ocean from the Gulf of Aden to the Bay of Bengal and also occur in the Indonesian archipelago and the Philippines. The landings of this important species in India have reached as much as 200 thousand tons per annum in some years, but the fishery is susceptible to irregular and large-scale fluctuations in resource availability (Table VII). For this reason, it has been studied intensively by fishery biologists in India, beginning in the early 1920s with the work of Hornell and his associates. As might be expected, the population over this vast area is divided into a number of probably reproductively isolated sub-populations, although these have so far been identified only by rather unsatisfactory meristic methods. Nair (1960) describes the main fishery for the species which is concentrated on the western coast of India, on the Kanar and Malibar coasts, where it is prosecuted within 8 or 10 miles of the shore by several different sorts of gear —gill-nets and drift-nets operated by canoes on which the freeboard has been extended upward by planking, and by large beach-seines. The shoals become available to the fishery towards the end of June, when populations of adults with mature gonads appear at the coast and progressively more northwards as the season advances; these fish have mature gonads and spawn during their first few months in the coastal region. As the season advances, a second wave of shoals arrives in the coastal regions and becomes available to the fishery; these are younger, immature fish and their availability reaches a peak during the months of October to December. By this time, the adults which arrived first have left the fishery which continues for a further couple of months into the new year. Approximately the same cycle of events is repeated annually on the east coast of India. The arrival of the first wave of adult sardines at the coast generally coincides with the onset of the southwest monsoon; at this time there is a very strong seasonal bloom of phytoplankton, principally of the diatom *Fragillaria* spp. and it is supposed that the spawning migration is timed to coincide with this; the arrival of the second wave of such shoals, at a peak in October to December coincides with a second phytoplankton bloom. Nair (1960) has shown that the stomach contents of this species are dominated by phytoplankton, largely a single species of the diatom (*Fragillaria oceanica*) and dinoflagellates. He has suggested that the large and important fluctuations in the availability of the species from year to year may be dependent upon the nature and timing of the annual bloom of this diatom. Although the oil-sardine occurs throughout a very wide area of the western Indo-Pacific, nowhere else does it appear to form such large concentrations as those that occur on the west coast of India; in the Philippines and Indonesia, for instance, it supports minor fisheries in many localities, but nowhere is it the object of single-species fisheries of the magnitude of those on the Indian coasts.

TABLE VII

Landings of oil-sardine on the west coast of India, 1948–1968; (from Panikkar and Jayaraman, 1967).

Year	Landings (metric tons × 10^3)	Year	Landings (metric tons × 10^3)
1948	1.2	1959	69·2
1949	0·3	1960	189·0
1950	34·4	1961	167·9
1951	17·2	1962	110·3
1952	13·9	1963	63·6
1953	51·8	1964	274·3
1954	33·9	1965	262·0
1955	30·4	1966	252·8
1956	7·4	1967	259·1
1957	191·5	1968	301·4
1958	123·3		

From Indonesia and the Philippines to the Arabian Sea, a number of other species of *Sardinella* are the object of small, local multi-species fisheries; the most important species involved in these appear to be *S. gibbosa* and *S. albella*, which together form the basis of the choodai fishery of Palk Bay on the Indian coast each summer, when juveniles of both species are taken with cast-nets, gill-nets, and traps of various sorts. *S. fimbriata* and *S. sirm* join the above two species in local fisheries in the Philippines, in the Visayan Sea in Indonesia, along the north coast of the Arabian Sea, and along the north coast of the Australian continent. These are mostly zooplankton-feeders and where their diet has been investigated (as by Ronquillo, 1960, for a number of species in the Philippines) it is evident that they subsist upon a mixed diet, dominated by crustacea of various sorts, according to the relative availability from place to place and season to season. A number of fisheries for small anchovies have developed throughout this great region and these are apparently mainly based upon the genus *Stolephorus*. In the Philippines two species (*S. commersoni* and *S. indicus*) are important, while in the Indian Ocean, as for instance at the Seychelles, *S. delicatus* appears to have some significance.

Besides the fishery for the oil-sardine, those for the various shads of the genera *Hilsa* and *Macrura* are also very interesting, and particularly that for *Hilsa ilisha* in India. Species of these genera occur in the river fisheries of Madagascar, off the eastern coast off Africa, of India, and in the East Indian archipelagos. The Indian fishery has been extremely well studied by the Pillays, husband and wife (see Pillay, 1958). They have shown that on morphometric and meristic grounds several stocks of *Hilsa* can be identified in the various river systems of the Indian subcontinent and this confirms the traditional ability of Indian fishermen and fish traders to distinguish fish of this species from different river systems in India by their taste, which as they point out, appears to be largely dependent on the fat content of the fish. Work on the genetic basis of the racial differentiation has been started by a study of the extent of individual serological variations in *Hilsa ilisha* of the Hooghly River. The distribution of the species extends from the Arabian Sea, including the Persian Gulf and the Red Sea, through the Bay of Bengal into the South China Sea and it occurs in estuarine areas and brackish lagoons throughout the whole of this area. Outside the spawning season the adult and maturing stocks are largely found in lower estuarine and inshore continental shelf regions of brackish water but do not occur significantly in the open ocean; during the breeding season the fish migrate upriver, and after spawning return to the estuarine region again, behaving like any other anadromous fish; as might be expected, in some of the major rivers such as the Ganges and the Brahmaputra, there are stocks which do not descend to the estuaries in the non-spawning season and these may be comparable with the lagoon-locked stocks of *Ethmalosa* already discussed for the coastal lagoons of the Guinea coast (p. 358). The stimulus for the upstream spawning migration depends upon the occurrence of flood-water, whether caused by the southwest monsoon or by the spring thaw in the northern mountains. In general, the upstream migration commences in the early spring and is over by the end of summer. Spawning of planktonic eggs occurs fairly high up the rivers some hundreds of kilometres from the estuaries which the adult fish have left, and juveniles descent progressively back to the estuaries and inshore areas, normally to reach the sea before they are one year old. The commercial catches of adult *Hilsa* usually include between three and five year-classes of adults and maturing fish. Fishing occurs primarily in shallow regions and especially in estuaries and the lower parts of riverine systems during the upstream migration of the fish. The main fishery season is, therefore, in the early part of the monsoon flood and varies from place to place and from river to river. A great many types of fishing gear and devices are used in the estuaries for the capture of *Hilsa*; cast-nets are thrown by men standing upon tiny platforms on a row of poles across the river while various forms of beach- and boat-seines, drift-nets, and gill-nets are worked off the mouths of the estuaries. The total catch of *Hilsa* for the Indian subcontinent in a successful year approaches 40×10^3 tons.

Such are the fisheries for various species of herring- and sardine-like clupeoids in the tropical region of the western Indo-Pacific; the main production, apart from the major fisheries for the Indian oil-sardine, is in the coastal regions of southeast Asia, southern China, the Philippines and northern Australia, a region with a multitude of islands, great stretches of shallow continental shelves, and of innumerable estuaries, lagoons, and bays.

The occurrence of major fisheries throughout this region is dependent on the position of major upwellings together with their coincidence with large populations of people with a sea-going tradition. The locations of major coastal upwellings and regions of eutrophication have been identified piecemeal during the last several decades, and it has become evident that the most important are those along the coasts of Somalia and southwest Arabia during the southern monsoon (see, Banse, 1968) together with the shallower upwelling along the west coast of India during the same period of the year; in the Indonesian region, Wyrtki (1962) has described a dome-like phenomenon in the thermocline topography which induces strong upwelling to the south of Java. Cushing (1969) has recently reviewed these regions and quantified the annual amount of production in each region. The alternation of the northerly and southerly wind systems, and the complex geography of the monsoon regions of southeast Asia and the archipelagos are responsible for the occurrence of very many regions of minor upwelling, most of which are very little known for their biological or fisheries significance.

The occurrence of a major fishery for the oil-sardine (*S. longiceps*) on the Indian west coast and the absence of a fishery of such magnitude in Somalia and southern Arabia may be largely due to the pattern of distribution of the human population rather than that of the fish resources. Though it is little documented, there are indications of abundant stocks of clupeoid fish, including the oil-sardine and other species of *Sardinella* in the northwest Arabian Sea and it appears that the sparse population inhabiting the desert coast of southern Arabia are heavily dependent on these stocks for their protein supply and for a crude form of animal feed; cast-netted *Sardinella* are dried in the sun on the sand and used as camel-fodder in some areas, for instance. Only about 30×10^3 tons of *Sardinella* appear to be caught at the present day in the northwest Arabian Sea, or less than a tenth of that taken in good years on the west coast of India, although Cushing (1969) estimates about four times as much primary production off Somalia and Arabia as on the Indian coast. The estimate by F.A.O. of about 800×10^3 tons as the fishery potential of the northwestern Arabian Sea, most of which may be expected to be pelagic clupeids, does not therefore seem unreasonable. Direct fisheries exploitation of this region is urgently required for an understanding of the future major fisheries of the world.

There are also indications (see Soerjodinoto, 1960) of major clupeoid resources associated with the Java–Sumatra upwelling region; the species involved here seems again to be the oil-sardine (*S. longiceps*) which is here known as lemuru. A minor fishery has developed for this species in the region of the Bali Straits, where the appearance of the fish, as on the west coast of India, is very seasonal; the season opens in September or October with the arrival of small fish, the larger fish arriving towards the peak of the fishing season in December and January at the height of the rainy season.

WESTERN PACIFIC

The North Equatorial Current on reaching the area of Indonesia and the Philippines, swings to the north and becomes a western boundary current sweeping along the eastern coast of Asia, along the mainland of China, and passing Japan as the Kuroshio or Black Current. Comparable with the western boundary currents off the east coasts of North and South America, this current contains a resource of clupeoids in which several species of *Sardinella* dominate along the mainland of China while off Japan, in the rich boundary zone between the warm Kuroshio and the cold southward-flowing current Oyashio, there are important resources based upon another pair of species, one sardine and one anchovy, such as we have seen elsewhere (p. 371): in this area, the species involved are *Sardinops melanosticta* and *Engraulis japonicus*.

Along the southeastern coast of the mainland of China at the port of Hong Kong, information on the clupeoid landings are easier to obtain than elsewhere. They are dominated by a species known in the literature as *Sardinella aurita*, called at Hong Kong the golden sardine, but which is probably different from the species which bears the same name in the literature from the warm parts of the Atlantic and Mediterranean Seas; the ecology of the *S. aurita* of Hong Kong appears to be quite different from that, for instance, in the Gulf of Guinea. At Hong Kong, this species is not strongly related in its ecology to an upwelling region but has a similar ecology to the many other zooplankton-feeding *Sardinella* that occur in the western Indo-Pacific (Li Kwan, 1960). It is present in large numbers in schools off Hong Kong during winter from December to April although the fishing season for juvenile schools begins in May and ends in November, thus extending over the summer months. In spring, the shoals of adult *Sardinella* leave the Hong Kong region and pass towards the north where there is a fishing season for it off Formosa during the summer months. This is a relatively long-lived fish, about six to eight year-classes being present in the fishery. The 0-group fish occur close to the coast where the specialized fisheries for them occur in shallow water.

The fishery for adult *Sardinella* is by large purse-seiners which range from the coast; these seiners are big wooden sailing junks carrying four smaller boats or sampans: two of these shoot and haul the net, while the other two drive the shoals of *Sardinella* into the circle made by the seine. Elsewhere in the region the fishery for *Sardinella* spp. depends quite largely upon attraction to lights at night and although this is probably a very ancient fishery it can only have become as efficient as it is at present with the introduction of powerful incandescent gas lamps at the turn of the present century; in Indonesia, the same sort of fishing until a very few years ago was still carried out by primitive torches and it is quite likely that this technique continues to be used in out-of-the-way areas of the western Pacific archipelagos.

Li Kwan (1960) describes the various non-industrial fisheries then operating throughout the western tropical Pacific for 11 species of *Sardinella*, including *S. aurita* and *S. longiceps*. None of these are on a very large scale and typically several species are included in the catches—he speaks also of mixed-species schools, though the evidence for this is not very clear.

Further to the north, the Japanese clupeoid fisheries, although not tropical, are well enough investigated and understood to be worth discussing briefly here. The fishery for clupeoids has the common name of the 'Iwashi' fishery and is a multi-species fishery based primarily upon the sardine (*Sardinops* *melanosticta*) and the anchovy (*Engraulis japonicus*) together with the round-herring (*Etrumeus micropus*); the addition of this third species to the Iwashi fishery places this region apart from those which we have already discussed in the eastern boundary currents of the Atlantic and Pacific Oceans. The Iwashi fishery reached a peak of more than $1{\cdot}1 \times 10^6$ tons, or 42% of the total fish landings in Japan, in the 1930s but has since declined to about half this figure; in the early 1960s it comprised only a little more than 10% of all fishes landed by the Japanese near-water fishing fleet. During the period of high catch and landings of the 1930s *Sardinops* made up the bulk of the landings, and the anchovy contributed only a few per cent. Fluctuations in the Iwashi fishery of Japan have been recorded in the half-millennium since the fishery was founded about the year 1500 (Uda, 1960); the present decline is the third such major decline recorded during this period. The decline in the sardine component of the Iwashi fishery in the last three decades has not been confined only to Japan, but has also occurred in the Soviet Far East, off Korea, and in the Yellow Sea.

The ecology of *S. melanosticta* appears to be very similar to that of other species of *Sardinops* discussed previously (Anonymous, 1969); distinct subpopulations based upon meristic characters have been recognized in the species; spawning occurs offshore and initially the post-larvae feed chiefly upon microcopepods and nauplii, progressively feeding upon larger micro-zooplankton. Subsequently, diatoms form an increasingly important item in the diet, although at no time does phytoplankton appear to be entirely dominant; however, during phytoplankton blooms, Yoshida (1955) found that diatoms figure rather largely in the diet; heavy feeding in spring coincides with the period of plankton bloom. During the period of abundant sardines in the 1930s it was known that the population undertook a complicated migration pattern around the Japanese Islands, although this can no longer be traced under present conditions of great scarcity of *Sardinops;* spawning apparently occurred and most of the stock originated near the southern tip of the island of Kyushu and the 0-group fish passed northwards along the Kuroshio Current to the Boso Peninsula passing their first year of life on this section of their migration pattern; in the following year the I-group migrated northwards during the summer to the island of Hokkaido and in the autumn of their second year of life migrated southwards again to winter around the Boso Peninsula. In their third year of life the same northward migration off Hokkaido occurred, but in this autumn these II-group fish passed rapidly southwards across the Japan Sea to the spawning area at the southern tip of the Island of Kyushu where they underwent their first spawning activity. In subsequent years the pattern of a northward migration to Hokkaido and Korea and a southern migration in the autumn to the Kyushu region was repeated. As the *Sardinops* stock declined during the 1930s to its present very low level, so the stock of anchovies appeared to increase and in the early part of the 1960s had risen from 9% of the landings from the Iwashi fishery in the early 1940s to almost 70% in the years around 1960. The remaining 30% of the catch is now comprised of juvenile and post-larval stages of all three species, together with a few other species not named here, which are together known under the commercial name of sirasu.

The distribution of *Engraulis japonicus* extends south to Formosa and somewhat north of the Japanese Islands but it appears that the main stock is in the region of Japan. Ecologically, it is extremely similar to those species already discussed, feeding upon all available microplankton including small crustaceans and large plant cells; it is evident that we have here a situation extremely similar to that which we have discussed in greater detail in relation to the California Current and to the Benguela Current off the west coast of southern Africa (p. 373, p. 363). A multi-species fishery appears to be easily thrown out of balance so that the dominance of one species is replaced by the dominance of another and (in this case at least) the overall production of the fishery appears to decline concurrently with the change-over in dominance of one species to another. The historical record of the Japanese sardine fishery and the palaeontological record for the California sardine both indicate that these species pairs may fluctuate in abundance either relatively or absolutely (or both) without a heavy fishing pressure having developed on the preferred species; that fluctuations in relative or combined stock size can occur in unexploited populations does not, of course, suggest that under other circumstances the role of heavy fishing pressure in triggering the decline of a *Sardinops* population may not have been decisive, as it apparently was off California. In the South African, the Californian, and perhaps in the Japanese case, there is evidence which indicates that the recent declines have been triggered by fishing pressure on a population made vulnerable by climatic events.

The presence of a major sardine population off Japan only occurs when 'warm' oceanographic conditions obtain, that is, when the influence of the warm Kuroshio water is greatest around the Japanese islands. Uda (1960) shows how relatively good and poor decades in the last half-century are correlated with warm and cool oceanographic conditions and although it has been suggested (e.g. by Aikawa, 1943) that the heavy fishery which developed on the whole oriental sardine stock alone caused the decline, it seems more likely that the failure of recruitment in the years 1938–1941 were primarily caused by environmental changes. As Uda (1960) has pointed out, in the late 1930s the pattern of currents changed to such an extent around Japan that the migration patterns of the sardines were modified and spawning occurred in areas which would place the 0-group fish in a precarious situation with the onset of winter cooling. The changed location of the present centres of population (Nakai, 1960) tend to confirm the effect of environmental rather than fishery changes.

In the southern hemisphere in the warm temperate regions of Australia and northern New Zealand a similar pair of species *Engraulis australis* and *Sardinops neopilchardus* occur. Fisheries for both species in this region are trivial and only a few hundred tons at most are landed annually; the ecology of both, as they have been described by Blackburn (1960), appears to be rather similar to that of similar species discussed in greater detail previously and it is possible that these resources, which are certainly under-utilized, might support fisheries of some significance in the future.

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712

R: Crustacean Resources

A.R. Longhurst

This section originated in the discussions of the *ad hoc* Working Party on the FAO Indicative World Plan (IWP), Survey of Crustacean Resources, which convened at the FAO World Scientific Conference on the Biology and Culture of Shrimps and Prawns in Mexico City between 12 and 24 June 1967. This Working Party consisted of the following participants, together with observers:

Appolonio, S.
Boschi, E. E.
Broadhead, G.
Butler, T. H.
Cadima, E. L.
Chapa-Saldaña, R.
Chittleborough, R. G.
Ellis, R. W.
Gneri, F.
Hall, D. N. F.
Hancock, D. A.
Holthuis, L. G.
Ivanov, B.
Johnson, D. S.
Kutkuhn, J. H.
Lindner, M. J.
Longhurst, A. R. (Convener)
López, M. T.
Massuti, M.
Obarrio, J. L.
Rasmussen, B.
Simpson, A. C.
Simpson, J. G.
Squires, H. J.
Slack-Smith, R. J.
Tiews, K. F. W.
Weber, D.
Williams, A. B.

The task of the Working Party was to review the first draft of the crustacean document which had been prepared by John Gulland (FAO Rome) and to accomplish this the Working Party decided to appoint a number of people as Regional Reporters with the responsibility of contacting individuals and organizations within their geographic area in order to obtain current data on the status of stocks of prawns and shrimps on a world-wide basis.

The Regional Reporters were as follows:

I Northwest Atlantic—Squires, Appolonio
II Northeast Atlantic—Simpson, A.C.
III Mediterranean—Massuti
IV(a) Northwest Pacific—Ivanov
IV(b) Northeast Pacific—Butler
V Western Central Atlantic—Lindner
VI Eastern Central Atlantic—Longhurst
VII Western Indian Ocean—Hall
VIII Eastern Indian Ocean—Hall
IX Western Central Pacific—Johnson
X Eastern Central Pacific—Ellis
XI Southwest Atlantic—Boschi
XII Southeast Atlantic—Longhurst
XIII Southwest Pacific—(vacant)
XIV Southeast Pacific—Hancock

The Regional Reports were all received by the Convener by the end of 1968, and were then consolidated into a reasonably uniform style of presentation to form the basis of the present draft. Only in exceptional cases, and especially with regard to crustacean resources other than shrimps and prawns, was reference made to material other than the reports submitted by the Regional Reporters; the present draft is not intended to be a review of the literature on the subjects covered, and is only as complete as the material submitted by the Regional Reporters. It was originally intended that the survey of crustacean resources should include data on three levels, namely: *present fisheries*; *potential fisheries*, e.g. those areas in which the presence of resources in good quantities is known by exploratory fishing; and *hypothetical fisheries*, e.g. areas in which the depths, type of bottom or other data suggested the existence of quantities of crustacean resources but which have not been confirmed by actual surveys. However, it was evident from the data included in the Regional Reports that this was not a valid division of the material and it was decided to present information at only two levels: that concerning *present fisheries production*, and that concerning the *potential for increased production* in the future; it is necessary here to define the manner in which two terms are used in this paper: *production* may be a rate or an amount and is intended to refer to the catches from a stock of crustacea, and *potential* is intended to refer to the production that may be expected from a stock in the foreseeable future, using fishing techniques which are expected to be available within this period.

An interesting discussion of the whole problem of estimating potential production from present-day data, and in particular from data derived from resource surveys, was received from M. J. Lindner, the Reporter for Region V. His points should be borne in mind when reading the estimates of potential contained in this paper, and it is useful to quote them *in extenso* here.

"At this point it may be useful to discuss methods for estimating potential harvest from areas about which we have limited information. Starting first with an area that has not been fished we might make guesses based on the range of a species or on the size of trawlable fishing grounds. Projections of the fishable magnitude of the stocks of shrimps based on these two methods are subject to such wide error that they are of little or no use. More knowledge than we now have is required to obtain any meaningful projection by these methods. It has been well established that shrimps do not distribute themselves uniformly over vast areas but concentrate in certain localized areas where presumably the temperature, substrata, and food are suitable.

"A slightly different situation would prevail if we also had information from exploratory fishing in an area; however, we would still not be in a position to make reliable estimates of potential harvests. Stock estimates of shrimp calculated from exploratory fishing *per se* approximate only the standing crop or, in other words, only the weight present at any one time. An estimate of the standing crop, consequently, may be highly deceiving if we attempt to use it to estimate the fishable magnitude of the stock, which means the total weight that can be produced from the stock during time intervals such as a year. We are primarily interested in the fishable magnitude of the stock rather than in the standing crop. We need to know how many tons we can harvest safely each year from the stocks. Obviously, we need more information than that provided by exploratory fishing if we desire good estimates of fishable stocks. This additional information may be ecological, involving knowledge of the life history of the feeding and nursery areas of species; it may be based on a comparison of the catch rates or landing data of the same or similar species with those in another area where intensive fishing is in progress; or, it may include the rates of growth, mortality, and recruitment.

"Precise measures of stock production must be based on growth, mortality and recruitment rates. These rates however are difficult to get and, indeed, may be impossible to obtain even though the species is heavily fished. The first two approaches, that is, using ecological data or catch data usually do not require the sophisticated methods involved in arriving at rates and frequently a combination of them can give fairly reliable estimates. It seems therefore that we need to start accumulating data on the first two subjects before we can project more accurately than now the fishable magnitude of shrimp stocks in areas that are not heavily fished."

For the reasons outlined above, and from the inconsistent nature of the data available, the estimates of potential production which are contained in this draft cannot be called other than educated guesses; this has been emphasized throughout, and wherever possible a conservative outlook has been taken with regard to estimates of potential production.

The bibliography which concludes this paper has been condensed from the regional bibliographies supplied by the Regional Reporters; it was felt by the Working Party in Mexico City that the value of this document would be greatly increased by the inclusion of comprehensive regional bibliographies, and an attempt has been made to do this for at least some regions.

An attempt has been made to standardize the use of scientific names throughout this draft, but it is certain that some taxonomic confusion is included, especially the reference to a single species by several names, and this was perhaps inevitable from the nature of the material on which the paper is based.

Crustacea are ubiquitous in their occurrence in the sea; they occur in the deepest abyssal benthic communities, in the plankton at all latitudes and all depths of the ocean, and in coastal waters, estuaries and lagoons. Apart from the unicellular animals, marine crustacea are probably, as a group, the most numerous animals on the planet, and they may constitute, as a group, the greatest animal biomass. The following approximate calculations, while not in any sense intended to indicate seriously the production of crustacea of all sorts which might be attained at some time in the future, serve to indicate the magnitude of the crustacean biomass in the oceans. If one considers only the planktonic crustacea, dominated by copepods, sergestids and euphausiids, and if one considers only the plankton of the upper 100 m of the ocean, it is probably near the truth that 100 g of plankton occurs on the average beneath each 10 m^2 of the sea surface. Extrapolating, this gives us 10 tons beneath each km^2 or 3.6×10^9 tons in the upper hundred metres of all the oceans, at any one time. Again, making some slightly dubious assumptions, one may take a value of 80% of this total plankton biomass as being composed of crustacea, and one may conservatively estimate that 50% of the total standing crop at any one time could in theory, be removed by man from the stock over a period of 1 year, providing that natural mortality by other organisms was somewhat under man's control. This gives a potential production of 1.4×10^9 tons annually, or about 30 times greater than the present production of all forms of animal material by the world's fisheries.

The purpose of this estimate is rather to indicate to what extent the presently exploitable crustacean resources are an extremely small part of the total crustacean biomass in the oceans. According to FAO fishery statistics the total world production of crustaceans in 1965 was approximately 1.2×10^6 tons, a figure approximately 1,000 times smaller than the estimate given above.

For the purpose of the present document we are ignoring all crustacean resources which are not likely to be exploited or exploitable within the next decade to any significant extent; because of the extremely tenuous nature of any arguments upon which potential estimates of the euphausiid populations of the ocean must be based, these are not included in the present consideration, even though serious study directed towards the exploitation of one species, *Euphausia superba*, has been begun in the Antarctic Ocean by the Soviet Union. It is felt at this juncture that the data on the potential from this type of resource are completely inadequate to estimate potential production, and euphausiids and similar stocks are not referred to in the body of this draft. (See also Section O, Antarctic).

The biological nature of the crustacean resources which are currently exploited in the ocean is very diverse both as to ecology, and perhaps more important (from a fisheries management point of view) with regard to such biological parameters as rates of growth, mortality and fecundity. Although many of the important crustacean resources occur in warm water, have extremely rapid growth rates, and are virtually annual species, some other important resources, especially those of high latitudes or of deep water, are extremely slow growing and have slow rates of recruitment to the fisheries. The management problems of these two different types of resource are, of course, very different, and too much extrapolation from one type of crustacean resource to all types of resources is to be avoided.

Crustacean resources are also extremely different in the amount of usable meat which is yielded by the processing of various forms; the yield may vary from as low as 8 to 10% in the case of the Chilean langostino to as high as 60 to 70% in some of the fisheries for large penaeid prawns. The figures used in the tabulated data in this text all refer to whole live weight, and to each species should be applied a factor, unknown in most cases, which would translate these into data referring to the usable meat yield.

The crustacean resources discussed in the following text may be categorized as follows: (1) lobsters, spiny lobsters, and similar forms—*Homarus*, *Nephrops*, *Palinurus*, *Panulirus* and *Jasus*; (2) crabs of a number of different forms, king crabs (*Paralithodes*), Tanner crabs (*Chionoecetes*), edible or market crabs (*Cancer*), portunid swimming crabs (*Callinectes*), and galatheid crabs (*Pleuroncodes*), etc; and (3) prawns and shrimps, including the high latitude and deep-water pandalids (*Pandalus*), the low latitude penaeid prawns (*Penaeus*), the caridean shrimps (*Palaemon* and *Macrobrachium*), finally the deep-water penaeid prawns of low latitudes.

Lobsters and Spiny Lobsters

The true lobsters of the genus *Homarus* occur on rocky coasts on both sides of the North Atlantic; they are rather slow growing, the females reaching first maturity at 5–8 years (depending on latitude) and the individuals remaining in the fishery for 12 years or more, and occasionally surviving to 25 or 30 years old. The adult females have a 2-year moulting cycle, alternating with spawning years, so that spawning and moulting occur in alternate years. The females carry the fertilized eggs for from 10–11 months before releasing the larvae into the plankton, for the relatively short planktonic life of 4 or 5 larval stages. Evidently, this is a relatively slowly renewing source and in common with all fishery resources in which the individuals which are relatively long lived the fishery is not very productive in the sense that only a small proportion of the total standing crop or biomass may be removed annually on a sustainable basis. Probably for this reason, the lobster stocks are generally approaching an overfishing situation.

The Norway lobsters *Nephrops* spp. are much smaller organisms which occur on rather deep muddy bottoms in many parts of the world, having been recorded in the North Atlantic, the Indian Ocean and the Northeast Pacific. There are very few biological data on this genus, and as a whole the fishery exploits the stocks only rather lightly.

The spiny lobsters or rock lobsters of the genera *Palinurus*, *Panulirus* and *Jasus* occur in rather lower latitudes than *Homarus* and species of these genera are ubiquitous in occurrence on hard substrates throughout the warmer parts of the ocean, forming in the tropics a very characteristic component of the reef fauna, though *Palinurus* appears to be a component especially of rather soft deposits compared with *Panulirus* and *Jasus*. Despite this wide distribution, commercial concentrations occur relatively sparsely. Growth rates probably vary widely from species to species, and at least in the tropical oceans members of these genera are probably much faster growing than are the high latitude lobsters of the North Atlantic. Females carry their fertilized eggs and remain in berry for less than two months after the spawning season. The eggs hatch in the spring in latitudes in which the winter has ecological significance, and characteristically pass through a rather large number of planktonic stages. This planktonic phase may occupy periods of almost a year in some species, and this fact is probably of considerable importance when the aquiculture of these genera is being considered, and it may well prove more difficult to rear them commercially, than species of the genus *Homarus*.

Crabs, King Crabs, etc.

The edible crab, *Cancer pagurus*, of northern Europe has a biology which is probably typical of generalized crabs which are important in fisheries the world over. In this species, first maturity occurs at a carapace width of about 13 cm, or an age of 4–5 years, and subsequently the females spawn in alternate years. The species performs rather well marked seasonal migrations, occurring inshore during the summer and offshore in deeper water during the winter; during the inshore phase in June to July the eggs carried by the females hatch and the larvae enter the inshore plankton. In the atuumn the crabs moult and the large females move offshore where in deep water in December and January spawning occurs, the eggs being carried by the female from then on through an inshore migration in the early spring, in April and May, to be hatched again in shallow water the following year.

The king crab, *Paralithodes camtschatica*, of the North Pacific is a large anomuran crab (of spider crab form) occurring in water to 250 m deep, −1° to 12°C. It is of rather slow growth, females maturing at a carapace length of 90 mm or at an age of 5–6 years. They spawn in the spring and carry eggs until the following spring when the larvae hatch into four planktonic stages in the months of March to June. The females spawn in shallow water and then return into deeper water, and the pelagic phase has a duration of about two months after which they descend into the benthic community. Female crabs molt annually after the eggs hatch, and just prior to mating. Males molt less frequently as they grow older, only once every three years for big crabs. King crabs live up to 15 years or more. Again, as in the case of the North Atlantic lobster, this is a resource which has rather a slow rate of renewal.

The brachyuran Tanner crab, Chionoecetes spp., which although it is only rather distantly related to the king crab has somewhat similar appearance, also has a somewhat similar ecology; the females mature at a carapace length of 8 cm at a rather advanced age carrying their eggs for 5–7 months and having a relatively short larval period.

The portunid swimming crabs, characterized by the blue crabs of tropical seas (*Callinectes*) are much more rapidly growing species than those discussed above and although their biology is rather poorly known it is probable that most of the low latitude species are essentially annual, and similar to the tropical prawns discussed below.

Prawns and Shrimps

The prawn resources of high latitudes in both the Pacific and Atlantic Ocean are dominated by pandalids of which the biology of *Pandalus jordani* in the Northeast Pacific Ocean is typical. This species is a protandric hermaphrodite in which sex reversal regularly occurs. The larvae are pelagic and occur in the coastal plankton, not entering estuaries or lagoons preferentially. At 2–3 years old the juveniles mature into male individuals and in the third or fourth year of life these individuals change into females. There is rather low fecundity from 1.0 to 4.0×10^3 eggs per female, which bears one brood of eggs per year at which time a high female mortality occurs. The females carry their eggs over the winter for a 5–month period, and release them into their 3–month pelagic stages in the early spring. The adults die after 2–4 years of life, although in lower latitudes the fishery may include only 2–3 year olds.

Pandalus borealis occurs in the entire boreal and has a very similar biology to *Pandalus jordani*, but the first male maturity occurs only in the second and third year of life and the females are 4–5 years old. A small percentage of females mature directly at 1.5 years old. *Pandalus montagui* of the Northeast Atlantic has a rather similar biology and it is certain that most of these pandalids have a relatively high longevity when compared with the shrimp resources of the shallow water and low latitudes. The pandalid resources of high latitudes appear to exhibit submergence towards low latitudes, and throughout the tropics wherever prawn surveys have been carried out on the upper part of the continental slope pandalid resources, more or less abundant, have been found together with a number of deep-living penaeids. The biology of these deep-living pandalids and penaeids is apparently completely unknown.

A number of crangonid shrimps occur in all latitudes and the European shrimp, *Crangon crangon*, may be taken as a rather typical example, although the lower latitude species of *Palaemon* and related forms presumably have rather more rapid growth rates and are certainly, in general, annual species. Pelagic larvae of *Crangon crangon* occur in the plankton from December through August and the adult individuals, unlike the pandalids, are heterosexual although one worker has suggested the occurrence of hermaphroditism in this species. Maturity occurs in the first or second year of life and three broods per year per female appear to be normal. The eggs are carried by the females during the spring to summer months for short periods of 3–4 weeks after which they hatch. Males appear mostly not to survive beyond their second year of life and females beyond their third year.

The resources of penaeid shrimps which occur on continental shelves in low latitudes are heterosexual and the females do not carry the eggs, but these are released into the water as soon as fertilized. The most significant ecological difference between the various species is whether or not the pelagic larvae and post-larvae remain in the coastal, continental shelf plankton or whether they preferentially enter brackish water in estuaries and lagoons, there to pass their juvenile period. Typically, as with *Penaeus duorarum* of the tropical Atlantic, and *Penaeus monodon* and *Penaeus indicus* of the Indo-Pacific, the females have rather long spawning periods throughout the year during which one or more peaks of spawning occur; the number of individual spawnings per female during the course of the season is not known in most cases. Fertilized eggs and early larvae can be found of all these species in the neritic plankton, but the early larvae very rapidly concentrate around lagoons and estuaries and enter on the floodtide. The larvae are at first transparent, and pelagic in the lagoons, but very early settle on the vegetation in shallow water and progressively, as they grow, move into deeper water within the lagoon. Mostly, the larval and juvenile forms spend less than one year in their brackish water environment, at the end of which period they return to the continental shelf where spawning occurs. There are indications in a number of species with this kind of ecology that the life span is only 12–14 months and that the adults die rather soon after returning to the continental shelf and spawning. In this case the large biomass of adults and near adults which are exploited on the continental shelves in the great shrimp fisheries of the world must consist of an ephemeral stock with a very rapid turnover, new individuals being consistently recruited from the nearby estuaries and lagoons.

However, a number of species do not have this ecology; such species occur in regions, such as the Persian Gulf, in which there is little possibility (because of the nature of the geography of the region) for the larvae to enter brackish lagoons, or they may occur alongside species whose larvae regularly and preferentially enter brackish water. Examples of the first kind of species are those which occur, as suggested above, in the northwest part of the Indian Ocean, in the Red Sea, the Persian Gulf and the northern part of the Arabian Sea, where coastal lagoons and other brackish water environments are extremely limited or absent. Examples of the second sort, in which larvae do not enter estuaries even though these are available for entry are *Parapeneopsis atlantica*, and *Xiphopenaeus kroyeri* of the eastern and western tropical Atlantic respectively, and also *Penaeus latisulcatus* and *Penaeus esculentus* in northern Australia (Frank Alverson, personal communication). In the Gulf of Guinea *Parapeneopsis atlantica* is one of the most abundant inshore species of penaeid, occurring most abundantly on shallow muddy deposits off the mouths of estuaries and lagoons but, unlike is neighbour *Penaeus duorarum* which occurs on similar deposits, its larvae and juveniles are never found in the neighbouring lagoons and estuaries.

REGIONAL ASSESSMENTS

Region I—Northwest Atlantic

This region includes the west coast of Greenland and the Davis Strait, the eastern coast of Canada, and the coast of New England in the USA. Crustacean resources are rather poor in species, and the whole region, with the exception of the southern coast of New England, is influenced by the cold current which passes southwards along the coast of north-eastern North America.

A. *Lobster resources*

This is one of the two centres of production of the Atlantic lobster *Homarus*, which is here represented by *H. americanus*. Landings of this species have varied little in recent years, from an annual rate of about 32.0×10^3 tons:

Country	*1961*	*1962*	*1963*	*1964*	*1965*
USA	11.8	12.8	13.2	13.3	13.3
Canada	21.6	21.1	20.0	19.0	18.4

A slight decrease which can be detected since 1962 does not appear to be attributable to any decline in fishing effort and, combined with evidence for a continuing change in population structure (at least off New England) towards a predominance of young individuals, suggests that the stocks are capable of no significantly increased production; indeed, the evidence indicates that only by proper management will the present level be sustained. The consumer demand for this species is extremely high, and with prices rising very significantly industrial tendencies will be towards increasing effort.

In recent years, this species is being taken increasingly towards the south and in recent years has been trawled in deep water as far south as North Carolina (Frank Alverson, personal communication), in Region V, probably in response to a climatic change in the marine environment. What effect this may have in the future is not predictable.

B. *Crab resources*

A trace of blue crab (*Callinectes* spp.) occurs in the landings in the most southerly parts of the region, but the major crab resources is that of *Cancer irroratus*, the rock crab. In 1966, the US landings of this species amounted to 2.2 × 10³ tons. This crab occurs in considerable numbers along the eastern coast of Canada as far north as the Strait of Belle Isle (Squires 1966). There are also indications (Wilder 1966), that this species occurs also in deep water off eastern Canada, together with a spider crab (*Chinoecetes*) related to the Tanner crab of the Gulf of Alaska. It would seem altogether possible that a fishery to the extent of 10.0 × 10³ tons might develop on all these species combined in this region.

C. *Prawn resources*

The prawns of this region are mostly cold-water pandalids, often occurring in deep water, together with some shallow water palaemonids.

Stocks of *Pandalus montagui*, *Spirontocaris spinus* and *S. lilljeborgii* are known to occur, but their potential is not known, and they are only exploited incidentally to the fishery for *Pandalus borealis*, which is the principal product of the prawn fisheries in the Northwest Atlantic.

While the fishery for *P. borealis* is concentrated mainly off Greenland, in very recent years a start has been made in Canada, where in the Bay of Funday 0.3 × 10³ tons were taken in 1967. Resource surveys have proved shrimping grounds, at rates of from 100–800 lb per hour, to the southwest of Newfoundland and in the Gulf of St. Lawrence (Squires 1961). Although no estimates have been made, it is reasonable to assume a total potential in this rather large area of about 5.0 × 10³ tons eventually.

The potential appears to be about the same off New England, where a minor fishery has existed for decades, but has been subject to remarkable stock fluctuation and therefore in availability to the fishery. The high catches in years of abundance do not properly reflect the relative stock abundance vis-á-vis poor years; when a very strong year-class is recruited to the fishery the market and processing facilities become glutted, and the catch is thus limited.

Year	*Massachusetts* (*tons*)	*Gulf of Maine* (*tons × 10³*)
1960	· 1.0	—
1961	· 1.0	—
1962	16.4	0.1
1963	10.5	0.2
1964	3.1	0.4
1965	8.1	0.9
1966	—	1.7
1967	—	3.0

It seems rather likely that this fishery will in the near future reach a production of 5.0 × 10³ tons.

Off Greenland, the fishery for *Pandalus borealis* has built up very rapidly in recent years, most of this production coming from Disko Bay and other inshore West Greenland waters to the south. The landings from the Greenland fishery in recent years have been as follows:

1950—0.2
1960—1.8
1961—2.5
1962—3.3
1964—3.7
1965—5.0
1966—5.4
1967—5.6

Rasmussen suggests that a production of 7.0 to 8.0 × 10³ will be realized in another decade; the potential of 6.0 × 10³ tons guessed by Ivanov in 1964 had almost been attained by 1967; and Smidt suggests a potential of 12.0 × 10³ tons, and perhaps more if offshore grounds in the Davis Strait are exploited by big vessels.

D. *Total Regional potential*

The following tabulation of the estimates suggested above indicates that the total potential of the region may increase by approximately a third in the foreseeable future, reaching a total of 69.0 × 10³ tons.

	Present	*Potential*
Homarus americanus	31.7	32.0
Cancer irroratus (and others)	2.2	10.0
Pandalus borealis		
United States	3.0	5.0
Canada	0.3	5.0
Greenland	5.3	12.0
Pandalus montagui	—	5.0
Total	42.5	69.0 (tons × 10³)

Region II—Northeast Atlantic

The crustacean production in this region is more diverse than in the Northwest Atlantic, to some extent because this region contains a greater degree of ecological diversity, due to the effect of the Gulf Stream on the European coast at high latitudes, but also perhaps due to the longer development of the fisheries in this region in historical terms, because of greater human pressures.

The 1965 catch was partitioned among 12 species, as tabulated on p. 211.

A. *Lobster resources*

(i) Common lobster (*Homarus gammarus*)

Lobsters occur from northern Norway to the Bay of Biscay, and are found on most coastal and near-coastal rocky grounds. Nearly all are national fisheries and over

Lobsters	
Homarus gammarus	2.3
Palinurus elephas	1.4
Nephrops norvegicus	25.5
Crabs	
Cancer pagurus	7.9
Carcinus maenas	0.7
Portunidae spp.	0.4
Maja squinado	4.7
Prawns	
Pandalus borealis	19.9
Pandalus montagui	0.1
Crangon crangon	45.8
Palaemon serratus	1.8
Parapenaeus longirostris	7.4
Total	117.9 (tons × 10³)

90% of the yield is believed to be caught within 3 miles of the coast.

Present catch is small, about 2.0×10^3 tons, though the value is high. While most stocks are heavily fished there would appear to be scope for 50–70% increases in catches in Norway, United Kingdom and Eire by increased fishing in certain areas, including in deeper water, and better management in others (Thomas 1965). It is considered that there is little prospect of increased yields from Sweden, Germany, Holland or France.

Denmark used to produce over 150 tons per annum, in many years between 1930 and 1950, and it would seem possible that these levels could be achieved again by increased fishing.

The landings of this species, by country, in 1966 are tabulated below, together with an estimate of the resource potential.

Country	*1966 landings*	*Estimated maximum sustainable yield*
Norway	0.3	0.8
Sweden	0.1	0.2
Denmark	0.03	0.2
Germany	0.0	0.0
Holland	0.0	0.0
Belgium	0.0	0.0
Scotland	0.6	1.0
England and Wales	0.4	0.6
Eire	0.3	0.5
France	0.4	0.4
Spain	0.0	0.0
Portugal	0.0	0.0
Total	2.1	3.7 (tons × 10³)

(ii) Spiny lobster (*Palinurus elephas*)

Palinurus elephas is a southern species extending north to Eire, southwest England and the Channel Islands. It lives in very rocky areas with strong tides and occurs from about 10–200 m. It is caught in baited traps, and just recently by full-time SCUBA divers off southwest England.

Country	*1965 catch*
Eire	0.2
England	0.1
France	0.7
Spain	0.4
Portugal	0.0
Total	1.4 (tons × 10³)

There is very little information on the population dynamics of the species. Recent work in England and Ireland suggests that the populations there are recruited from further south (pelagic larvae? juvenile migration?) as animals below 2 lb weight are rarely seen, even by divers, and there are substantial long term variations in their abundances. Catches in Eire were of the order of 400 tons annually in the 1950s and 1960s and it is probable that 500 tons is nearer the average long term yield than the present 200 tons. The stock around southwest England is lightly exploited and could probably yield an average of at least 200 tons annually with increased effort. The potential of the French and Spanish grounds is not known but is likely to be somewhat above the present yields. The sustainable yield for the whole area is likely to exceed 2.0×10^3 tons.

(iii) Norway lobster (*Nephrops norvegicus*)

Nephrops norvegicus occurs in many areas from Iceland to the Mediterranean where the bottom sediments are a fine mud. Such grounds are typically in water over 120 m but in sheltered areas such as fjords, and where tidal currents are small (Irish Sea), *Nephrops* occur in depths as shallow as 20 m.

A number of new northern grounds have been exploited since 1939 with a steady increase in landings; 10.0×10^3 tons being landed in 1948 and 30.0×10^3 tons in 1964. It would seem probable that there are still some extensive populations which have not been exploited, especially at considerable distances from ports.

The habit of *Nephrops* to form burrows in the bottom and to remain in them at night (and also during full daylight in shallow waters) reduces the efficiency of capture and makes overfishing more difficult. There is little indication that many grounds are very heavily exploited, though recent declines in yield off Norway may be due to this. A decline in average size on some grounds off Scotland is probably due to fishing (Thomas 1965), but considerable increases in fishing effort off Iceland (Sigurdsson 1965) and continued heavy fishing in the Irish Sea (O'Riordon 1965, Gibson 1965) have not lead to decreases in average size of *Nephrops* in the catches in these areas.

The occurrence of *Nephrops* in the stomachs of cod over a wide area northeast of Scotland suggests that landings by Scottish boats from the North Sea could be about doubled to $5.0–10.0 \times 10^3$ tons per annum (Thomas, personal communication). It is also probable that landings from grounds around Ireland could be more than doubled (Gibson, personal communication).

While the stocks south of Norway may not be able to give a much greater yield it would seem probable that the sustainable yield from the Northeast Atlantic area as a whole could be about doubled to around 60.0×10^3 tons. However, it is possible that the most distant fishing grounds will not readily be fully exploited, as the larger boats may find it more profitable to catch fish than Norway lobsters.

The 1965 landings, by country, and the degree of exploitation are tabulated (p. 212).

B. *Crab resources*

(i) Edible crab (*Cancer pagurus*)

This crab is common where there is a rocky coastline,

Country	Area	Degree of exploitation	1965 production
Iceland	Near seas	Moderate	3.7
Faroes	Coastal areas	Light	0.1
Norway	Coastal areas	Light	0.2
Sweden	Kattegat	Heavy	0.3
	North Sea	Moderate	0.0
Denmark	Kattegat	Heavy	0.8
	Skagerak	Moderate	0.3
	North Sea	Moderate	0.0
Germany	Kattegat	Heavy	0.1
Holland	North Sea (by-catch)		0.0
Belgium	South North Sea		0.5
Scotland	North Sea (near seas)	Moderate	3.5
	West coast	Light to moderate	3.0
England and Wales	North Sea (near seas)	Moderate	0.4
Northern Ireland	Irish Sea	Moderate	0.9
Eire	Irish Sea	Moderate	1.0
	Celtic Sea	Light	0.0
France		Moderate	7.4
Spain	Near seas	Moderate	3.8
Portugal	Near seas	Light	0.2
Total			26.4 (tons × 10^3)

though, due to seasonal offshore migrations, considerable quantities of crabs are also to be found up to 10 mi offshore and into depths of 80 m on soft ground. Crabs are nearly all caught by baited traps, though some are caught as an incidental catch by trawlers.

Crabs are low-priced and therefore long-distance transport to markets is usually not economic. Recent developments have been towards regional processing plants, leading to deep-freezing and canning, which has stabilized fisheries and allowed their expansion away from major consuming centres. This process is progressing in several countries. The most heavily exploited stocks are on the British coast, but recent investigations show that the fishery is now taking about the maximum sustainable yield (Edwards 1967).

Country	1965 landings	Estimated maximum sustainable yield
Norway	3.4	5.0
Sweden	0.2	0.4
Denmark	0.0	0.1
Germany	0.0	0.0
Holland	0.0	0.0
Scotland	1.8	3.3
England and Wales	2.6	3.5
Republic of Ireland	0.1	0.5
France		0.5
Portugal	0.1	0.1
Spain	0.1	0.1
Total	8.3	13.5 (tons × 10^3)

It is possible that yields from Norway could be substantially increased as the average size of crabs caught there is large.

The maximum sustainable yield from the region is probably between 50 and 100% above the current yield of 8.0 × 10^3 tons, and a potential of 13.5 × 10^3 tons is assumed for our present purpose.

(ii) Shore crab (*Carcinus maenas*)

This crab is very abundant in coastal waters in the central and southern part of the area, being killed in shallow waters in the North Sea in severe winters. It is only exploited commercially in Spain and Portugal where a total of some 0.3 × 10^3 tons per annum are landed.

As it is a major predator on the young of a commercial species of mollusc, the development of a fishery for this species could benefit mollusc production. There is also a demand for "peeler" crabs of this species in Italy.

(iii) Spider crab (*Maja squinado*)

This species is common in the southern part of the area to the coast of Ireland and the Western English Channel and occurs also in the Mediterranean. At certain times of the year it aggregates (as does the Tanner crab in the North Pacific) into what are believed to be spawning piles, when large numbers can be caught by trawling. At other times they are usually caught by trapping. The meat yield is low during much of that year but the muscle tissue is sweet, and highly esteemed.

The present fishery is limited to France, Spain, Yugoslavia and Portugal and very small quantities in southern England, and separate landing statistics are only kept for Portugal. Present landings are 4.7 × 10^3 tons; this figure could probably be increased to about 6.0 × 10^3 tons.

(iv) Swimming crab (*Portunidae* spp.)

These crabs are common throughout most of the area but are only exploited by Spain. Potential yields are unknown.

C. *Shrimp and prawn resources*

(i) *Pandalus borealis*

This cold water (3–8°C) species occurs from north of Spitsbergen to the northern North Sea on clay and mud bottoms. It rarely occurs in quantity in water less than 60 m deep but extends to depths greater than 1,000 m. However, present day fisheries are limited to depths between 60 and 600 m.

Around Iceland the development of *Pandalus* fisheries has been only during the past decade and new grounds are still being found.

Present production is around 1.4 × 10^3 tons. This could be somewhat increased by reduced fishing in the

1965–1966 LANDINGS BY COUNTRIES

Country	*Iceland*	*Norway*	*Sweden*	*Denmark*	*Total*	*Potential*
Iceland	1.4				1.4	2.0
Faeroes					—	1.0
North Norway		4.4			4.4	6.0
Northwest		0.6			0.6	2.5
West		1.9[1]			1.9	2.0
South (Skagerak)		1.8[2]	1.5[3]	0.9[4]	5.1[5]	12.0
Kattegat				0.8	0.8	1.0
N. Sea Fladen				3.0	3.0	4.0
Farne Deep						1.0
Total	1.4	8.7	1.5	5.6	17.2	31.5 (tons × 10^3)

[1] 3.5 × 10^3 tons per annum in 1960–64
[2] 3.2 × 10^3 tons per annum in 1960–64
[3] 5.0 × 10^3 tons per annum in 1962
[4] 2.0 × 10^3 tons per annum in 1962–64
[5] 10.2 × 10^3 tons per annum in 1962.

most heavily fished areas (Skuladottir 1967) and extended new fisheries, giving a yield which might be somewhere about 2.0 × 10^3 tons.

There is no fishery for *Pandalus* at Faroe. There is no information on the occurrence of *Pandalus* in this area but from temperatures, depths and bottom types, useful populations can be anticipated.

Fishery for *Pandalus* off Norway started in 1897 following research by Johan Hjort. The fishery has continued to expand and 1,500 Norwegian trawlers of 30–80 ft now work the whole length of the Norwegian coast and offshore grounds down to 600 m, wherever the ground is of soft clay and mud. There is no evidence of overfishing but a minimum mesh of 30 mm throughout the trawl is in force to minimize destruction of young prawns (Rasmussen 1967).

In that part of the Norwegian Deep which extends along the south coast of Norway, Denmark and Sweden, with mean annual yields in 1965 and 1966 of 1.8, 1.8, and 1.5 tons × 10^3 respectively.

Five-year means of landings from off the Norwegian coast since 1950 were as follows:

	1950–54	*1955–59* (tons × 10^3)	*1960–64*	*1965–66*
North	1.0	2.0	3.2	4.4
Northwest	0.3	0.3	0.4	0.6
West	0.7	2.0	3.4	1.9
South				
(a) Norway	1.3	1.9	3.3	1.8
(b) Denmark	?	?	4.5	1.8
(c) Sweden	?	?	4.5	1.8

There appears to be some scope for further development, especially in northern Norway, and a mean total annual yield of about 20.0 × 10^3 tons is probably attainable without working into deeper water. The catches fluctuate partly as a result of variable year-class strength and partly from changes in water temperature, which can make the prawns leave the normal fishing grounds temporarily (Rasmussen 1967). Catches were down off West and South Norway in 1965 and 1966, but the maximum sustainable yield is probably slightly above the 1960–64 average 10.0 × 10^3 tons.

The Kattegat is only fished by Danish boats, which produce 0.2 to 0.8 × 10^3 tons a year. There seems little chance of raising this much above 1.0 × 10^3 tons as the grounds are all known and heavily fished.

Since 1960 Danish boats have been fishing the Fladen grounds of the North Sea and yields have been around 3.0 × 10^3 tons a year in 1965 and 1966. In 1967, German and Danish trawlers have started fishing the Farne grounds 15 mi from the coast of England but yields are not known.

(ii) Common or brown shrimp (*Crangon crangon*)

Total landings of shrimps for food and industrial uses from Germany and Holland have fluctuated between 4.0 and 70.0 × 10^3 tons in recent years. Increases in the size and efficiency of the Dutch fleet have been compensated by a reduction in the German fleet.

Crangon crangon is limited to estuarine and coastal waters between the Central North Sea and the Bay of Biscay, and also occurs in the Irish Sea. It forms important fisheries along the coast of Germany and Holland where extensive shallow sandy areas form its main habitat.

There is a substantial fishery in both countries for small shrimps for meal. Some increase in the weight of shrimps for human consumption can be expected by the use of larger meshes in the shrimp nets which would increase the efficiency of capture of the large shrimps as well as releasing small shrimps to be recaptured at a larger size.

At present Denmark does not permit fishing for shrimps within the 3 mi limit though the resources here could probably yield 1.0 × 10^3 tons per annum.

Dutch catches for human consumption could probably be increased by 50% by greater efficiency and the protection of small shrimps.

Catches by England in The Wash and in the Thames estuary could probably be increased to 1.0 × 10^3 tons by greater efficiency. The future of the Irish Sea fishery is uncertain due to the possible construction of a barrage across Morecambe Bay—the main shrimp fishing area—but annual catches from the whole of the Irish Sea could probably be maintained around 0.7 × 10^3 tons.

French catches have been increasing steadily in recent years

(tons × 10³)	
1960—1.4	1965—2.0
1962—1.8	1966—2.3

and it is probable that the sustainable yield is around the 1.5 × 10³ tons for the Channel and 2.5 × 10³ tons for the Atlantic coast, if not more.

The following tabulation summarizes present and potential production of this species:

Coastal waters of	*1966 production*	*Potential yield from known grounds*
Denmark	—	1.0
Germany	27.3[1]	28.0
Holland	14.7[2]	15.0
Belgium	1.0	1.0
Scotland	0.1	0.1
England N. Sea	0.8	1.0
Irish Sea	0.5	0.7
France		
English Channel	0.9	1.0
Atlantic	1.4	1.5
Total	46.7	49.3

[1] Includes 21.6 × 10³ tons small shrimps for industrial use

[2] Includes 6.5 × 10³ tons small shrimps for industrial use.

(iii) Pink shrimp (*Pandalus montagui*)

This species extends from the English Channel to the Arctic and is found on harder bottom in estuaries and into deeper waters. It does not grow to a large size, rarely exceeding the size of the brown shrimp, the larger shrimps having a count of around 400 to the kilogramme.

At present it is only fished commercially by Britain where catches during the past decade have been only a few tens of tons compared with hundreds of tons prior to 1958. The reduced catches have been due to a general scarcity of the species on the three main fishing grounds—The Wash, Thames estuary and Morecambe Bay due to causes unknown.

No attempts have been made to find fishable concentrations in other countries, but it is probable that such concentrations exist, especially around Scotland, Norway, Faroes, and Iceland, where it is known to be present. But, being a small species, requiring picking by hand, it is uncertain whether fisheries would develop even if substantial concentrations were found.

(iv) *Dichelopandalus bonnieri*

This prawn is present in quantities which could probably support a fishery in various localities on the West of Scotland and probably elsewhere.

No fishery exists at present and it is impossible without more information to assess its potentialities.

(v) *Palaemon adspersus*

This prawn is only fished commercially in the Baltic by Denmark where catches have varied between 60 and 340 tons in the last 5 years.

While this prawn also occurs in many areas it is unlikely to be able to support substantial fisheries anywhere.

(vi) Crevette rosé (*Palaemon serratus*)

Palaemon serratus is one of the larger palaemonid prawn reaching counts of 100 per kg. It is a southern species, the most northerly fisheries being in the English Channel and Wales where cold winters cause substantial mortalities. It lives among sea weeds on rocky coasts and on the adjacent sea bed being caught both by baited traps among the algae and by trawls. Yields are not likely to be great anywhere, but it is at present the subject for artificial rearing (MAFF, Conway, and commercial enterprise in England) which if successful could give substantial production.

Production in 1966 was as follows:

English Channel	<10 tons (Potential 10–100)
French Atlantic coast	700 tons (Potential 1.0 × 10³ tons)

D. *Total resource potential of Region II*

The following tabulation synthesises the various estimates and potentials discussed above. The rather surprising high potential increase in production rates which are suggested by these figures probably reflect rather the state of exploration of the region rather than that it is inherently rich in crustacean products. Such observations may be held to indicate that estimates made in rather poorly explored regions may very well be too low.

	Present	*Potential*
	(tons × 10³)	
Lobsters		
Homarus vulgaris	2.1	3.3
Palinurus vulgaris	1.4	2.0
Nephrops norvegicus	26.4	60.0
	(29.9)	(65.3)
Crabs		
Cancer pagurus	8.2	13.5
Carcinus maenas	?	?
Maia squinado	4.7	6.0
Portunus spp.	0.4	1.0
	(13.3)	(20.5)
Prawns, etc.		
Pandalus borealis	17.2	31.0
Crangon crangon	46.6	49.3
Pandalus montagui	0.1	0.1(?)
Dichelopandalus bonnieri	?	?
Palaemon adspersus	<0.5	0.5
Palaemon serratus	<1.0	1.0
	(65.4)	(82.8)
Total	108.6	168.6

Region III—Mediterranean and Black Sea

These inland basins are rather unproductive of crustacea and the extremely oligotrophic nature of their ecology suggests that their potential production relative to other sea areas is likely to be low; nevertheless, the 25.0 to 30.0 × 10³ tons of crustacea produced each year from this region is surprisingly high, yet this is probably only a reflection of the relatively highly exploited nature of the resources. As for fish, so for crustacea; the fishing pressure is probably extremely high relative to the low production rates of the marine resources as a whole in these seas.

The production statistics are extremely variable in their quality, and to obtain any overall estimate of present day and hypothetical production one must make many assumptions, perhaps more than in some other regions.

A. *Lobster resources*

(i) European lobster (*Homarus gammarus*)

There is a very small production of this species, scarcely exceeding 1.0 × 10³ tons annually, in the Mediterranean Sea, mostly taken by Italian boats, although this apparent national preponderance may very well be due to anomalies in the reporting methods of production statistics from various countries.

(ii) Norway lobster (*Nephrops norvegicus*)

This species appears to occur rather widely in deep water in the Mediterranean Sea and production is considerably higher than for the European lobster. Again, however, the main producing country appears to be Italy with Algeria, Spain, and Yugoslavia each adding rather smaller quantities to the total. The total production from the Mediterranean has remained extremely constant for the last decade, varying only between 2.0 and 3.0 × 10³ tons annually.

(iii) Spiny lobster, rock lobster (*Palinurus elephas*) = *P. vulgaris*

An extremely small quantity almost always less than 1.0 × 10³ tons annually, of this species, together with traces of *P. regius* (green rock lobster) are taken in the Mediterranean Sea annually. The catches are produced mostly by vessels from Algeria, France, Italy, and Spain although it is extremely likely that small quantities are taken by a number of other countries, but do not show in their fisheries statistics.

B. *Crab resources*

Extremely small quantities of various species of crabs are taken in the Mediterranean basin, appearing in the statistics of France, Spain, and of Yugoslavia. The total has never been recorded as exceeding 1.0 × 10³ tons annually and little expansion appears to be possible.

C. *Prawn and shrimp resources*

The bulk of the production of crustacea in the Mediterranean Sea is included in this resource category, the production of which has been rising slowly but rather steadily in recent year. From less than 20.0 × 10³ tons a decade ago the production is now approaching 25.0 × 10³ tons. This figure does not include shrimps and prawns which may be included in the statistical category "various marine crustacean" as reported by a number of countries, the total of which for the Mediterranean and the Black Sea basins is now approaching 10.0 × 10³ tons. It is to be expected that 50–75% of this total should be applied to production from the prawn and shrimp resources. The production statistics from most countries do not permit partition of the total production among the constituent species, and it is difficult to apportion relative importance to the species which are known to occur in the Mediterranean and Black Sea catches, and which are tabulated here.

Prawns and shrimps of economic importance in the Mediterranean and Black Seas; scientific and Spanish names

Gamba	
Parapenaeus longirostris	Gamba blanca
Solenocera membranacea	
Crangon crangon	
Gamba de Profundidad	
Aristeomorpha foliacea	Gamba roja
Aristeus antennatus	Gamba rosada (*Gambli rossi*—Mat.)
Plesionika edwardsii	Carabinero
Langostino	
Penaeus kerathurus	Langostino
Quisquilla	
Palaemon elegans (= *L. squilla*)	
Palaemon xiphias	
Palaemon adspersus	
(*Plesionika* spp. ?)	

Of the species tabulated above, *Parapenaeus longirostris* is probably the species of which the greatest catch is taken currently in the Mediterranean, and this is certainly true for those countries such as Spain, France, and Italy for which the statistical data are relatively sophisticated. Probably next in importance are the deep-living prawns (known in the Spanish fishery as gamba de profundidad) and it is probably this resource from which the greatest increase of production may be expected, although it is already rather well surveyed and is already under fairly heavy exploitation, particularly in the western basin of the Mediterranean from Italy and Sicily to the Straits of Gibraltar; *Aristeus antennatus* is the only commercial shrimp taken at Malta, where it occurs at 200–400 m on soft clayey deposits. These Central Mediterranean grounds already appear to have reached their maximum production (J. A. Galea personal communication). While both gamba and gamba de profundidad are known to be dominant in the landings of Spain, France, Italy, Tunisia, and Algeria, the langostino, *Penaeus kerathurus* (which is a penaeid of exceptionally large size, and which occurs also along the tropical West African coast) is important in some of the smaller fisheries because of the relatively high value of the individual prawns on the market.

The small shrimps of the genera Crangon and Palaemon are nowhere taken in large quantities; the largest production which is probably attributable to such forms appears to be that reported by Bulgaria where it has reached between 4.0 and 5.0 × 10³ tons annually.

In the Central Mediterranean the only shrimp fishing in the Adriatic is beyond 600 m depth, while in the Ionian Sea coastal fishing predominates; in the remainder of the region (Tyrrhenian and Ligurian Seas, and around Sardinia and Sicily) shrimp trawling occurs from the coast out to 600 m. It seems, from the rather dispersed statistics available that Italian catches (1967—10.0 × 10³ tons) dominate, and make up a large part of the total Mediterranean shrimp catches.

In the eastern Mediterranean, shrimp production occurs in only a few areas (Ivanov 1964) notably on both east and west coasts of Greece along the Turkish seaboard, on the coast of Israel, and off the Nile Delta.

The Greek production is based on *Penaeus kerathurus*, which forms 50% of the catch, together with *Parapenaeus longirostris* and *Palaemon elegans*. Catches are consumed fresh and locally and amount to almost 0.5 × 10³ tons annually. The Turkish production amounts to about the same figure annually and probably depends upon the same species.

The Turkish shrimp production extends from the Sea of Marmora (where no trawling, only traps, is permitted) to Adana in the east. The major exploited species are *Parapenaeus longirostris*, *Penaeus trisulcatus*, *P. semisulcatus*, and *Metapenaeus monoceros*, the last two of these being Indo-Pacific species which have migrated through the Suez Canal. Total production is less than 0.5 × 10³ tons and no data are available regarding specific composition of the catches. Until recently, Iskanderum Bay at the eastern end of the coast, was a major centre of production, but has now been fished out and the commercial fishery there has collapsed.

The Egyptian production is rather greater, and in 1957 the catches off the Mediterranean coast were about 2.8 × 10³ tons. In recent years (if one accepts Hall's estimate that 50% of UAR production comes from the Indo-Pacific, see p. 28) the production has been about 5.0 × 10³ tons. It is not known what species are represented in the catches. The effect of the Aswan High Dam will probably be to reduce production from this fishery.

D. *Total resource potential of Region III*

It is extremely difficult to estimate in an objective fashion the potential production in this region but it seems, from the stability of the landings, and from the general interest in the European markets in crustacea, that the relative level of exploitation is probably already rather high of fisheries as disparate as those in deep water around Malta and in shallow water in Iskanderun Bay, so that no great increase can be expected. As indicated earlier, any major increase will probably come from the deeper-living shrimps and prawns which, although their general distribution is now fairly well understood have only in recent years come under heavy exploitation.

Because of these facts it is not postulated that the landings could be expected to increase in the foreseeable future beyond 50.0 × 10³ tons altogether and this estimate may in fact be generous, but is a conveniently rounded number, to be used here as the potential. In fact, it represents a little more than a 20% increase on present production, and an increase of this magnitude may be quite realistic.

Region IV—North Pacific

This region encompasses the whole of the North Pacific from the cold waters north of Hokkaido to the California Current at the level of the Mexican border. Here the important members of the crustacean fauna are quite different from the crustacea of the warmer parts of the Pacific—pandalid shrimp replace penaeids, various spider crabs replace spiny lobsters, and swimming crabs are virtually absent.

A. *Crab resources*

The king crab (*Paralithodes camtschatica*) has been for many years the most valuable single-species crustacean fishery in the region, being taken by fleets from USA, USSR, Japan and Korea. The total landings of this species have shown the following development:

(tons × 10³)

1938—79	1962—103	1966— 150
1948—18	1963—112	1967— 131
1958—66	1964—120	1968— 111
1961—88	1965—132	1969— 86

The centres of production of king crabs have been: the Okhotsk Sea (and Tartar Strait, W. Sakhalin and N. Hokkaido); the Bering Sea; the Gulf of Alaska, especially near Kodiak. Traditionally, the US fleets have fished the Gulf of Alaska and some parts of the Bering Sea, while the USSR and Japanese fleets have occupied themselves with the stocks in the Okhotsk and Bering Seas; the division of the catch among the various fleets in some recent years was as follows:

Country	*1963*	*1964* (tons × 10³)	*1965*	*1966*	*1967*
Japan	31.6	31.8	25.9	31.0	30.0
Korea	2.3	2.2	0.3	0.4	1.5
USA	35.7	39.3	59.7	72.5	57.9
USSR	42.5	46.2	44.2	46.0	42.3
Total	112	120	132	>150.0	>132.0

There have been indications that the stocks in the Okhotsk Sea to the west of Kamchatka have seriously declined in recent years and it is unlikely that the potential production is greater than the present figure of 40.0–45.0 × 10³ tons together with less than 5.0 × 10³ tons of blue king crab (*P. platypus*); this fact, is however, not demonstrated in the catch statistics because the Soviet and Japanese fleets turned their effort elsewhere. A decline, which may be the result of the year-class fluctuation or may be due to overfishing, is now becoming evident in the data from the Gulf of Alaska. In the early 1960s, before any decline in availability became

PRODUCTION OF CRUSTACEANS IN RECENT YEARS AND FUTURE POTENTIAL MEDITERRANEAN AND BLACK SEA (tons × 10³)

	1958	*1961*	*1962*	*1963*	*1964*	*1965*	*Potential*
Prawns, etc.							
Crangon crangon	1.0	+	+	+	+	+	+
Others	19.0	21.0	21.0	21.0	22.0	23.0	
Lobsters							
Homarus gammarus	1.0	1.0	1.0	1.0	3.0	1.0	
Nephrops norvegicus	3.0	3.0	2.0	2.0	2.0	3.0	
Palinurus elephas	+	+	+	+	1.0	+	
Crabs							
Miscellaneous crabs	+	+	+	+	+	+	
Various crustaceans (Taxa not stated)	4.0	7.0	9.0	8.0	9.0	9.0	
Total	28.0	32.0	33.0	32.0	37.0	36.0	50.0

evident, the approximate distribution of the catch was as follows:

		(tons × 10³)
Okhotsk Sea	—USSR	31.1
	Japan	11.1
Bering Sea	—USSR	9.0
	Japan	13.5–18.0
	USA	+
Gulf of Alaska	—USA	59.4

The evidence for a decline in king crab availability has turned attention towards the Tanner crabs of the genus *Chionoecetes*. Three species are important in the North Pacific, and there is some evidence that their abundance may be linked to that of the king crab (Alverson personal communication), so that their availability has increased as the stocks of king crabs have decreased: *C. tanneri* occurs commonly in deep water from California to Washington, while *C. opilio* and *C. bairdi* occur in shallower water in the Gulf of Alaska. Species of this genus form about half the Japanese crab landings, and are exported under the name of "snow crab".

Also occurring in the region is the Dungeness crab, *Cancer magister*, of the western seaboard of North America, together with similar species on the Asiatic coast. The landings on the American coast follow, but similar data for the Asiatic coast are not available:

Country	*1963*	*1964*	*1965*	*1966*	*1967*
USA	11.3	10.5	12.2	18.1	17.7
Canada	1.5	2.0	1.6	2.1	2.4

The crabs *Lithodes aequishina* and *Geryon quinquedens* are also available and may have some potential in the region, though they are deep water crabs occurring at 300–1,000 m and may require the development of special techniques for its exploitation. A Japanese trap fishery at 300–500 m mainly now produces about 3.0 × 10³ tons per year of *L. aequidens*. Other species of crabs that could be commercially valuable are *Erimacrus isenbeckii*, *Telmessus cheiragonus*, and *Paralithodes brevipes*.

The recent decline in the availability of king crab suggests that the total potential of this resource may not be as high, on a sustained basis, as the highest annual catch rates recorded in the data. For this reason, a very conservative potential production of 100.0 × 10³ tons annually is used here. The potential production of the Tanner crab is harder to guess. It has been suggested that it may be as high as that of the king crab, but if there is ecological competition between these species their potential productions should be considered together. For this reason, the yield of Tanner crabs is guessed at being half that of king crabs when both are being exploited and a combined figure of 150.0 × 10³ tons for the two species is postulated.

The potential production from the Dungeness crab stocks is hard to estimate; the annual fluctuations in availability seem to be due to year-class fluctuations, and there seems to be no evidence of serious over-exploitation. An increase × 2 over present average production of 22.0 × 10³ tons is postulated for present purposes. It is assumed, also, that a same potential of *C. amphicetus* occurs on the Asiatic coast, though it is concealed in FAO production data, and a total potential of 50.0 × 10³ tons for the whole region is used here.

B. *Prawn resources*

The prawn and shrimp resources of the region are dominated by about six species of pandalid prawn and a small number of crangonid shrimps, of much lesser importance.

On the Asiatic coast, the pandalid catch off South Korea amounted to about 3.2 × 10³ tons in 1965, and was dominated by *Pandalus hypsinotus*; the North Korean catch, in which this species, together with some *Pandalus latirostris*, is again dominant, probably raises the total Korean catches to about 5.0 × 10³ tons. In the Okhotsk Sea the pandalid resources are known to be rich, but production has not yet begun. Here, *Pandalus goniurus* dominates, expect along the west coast of Kamchatka, where *P. borealis* becomes important. The potential of this area is not known, but is guessed to be at least 10.0 × 10³ tons annually.

The production statistics for the Bering Sea and the Gulf of Alaska are combined, and the composition of the catches are as follows: *Pandalus borealis* (80–90%), *Pandalopsis dispar* (5–15%), *Pandalus goniurus*, *P. hypsinotus* and *P. platyceros* (<5%). Annual catches for the whole of this area were:

Year	*USA*	*USSR* (tons ×10³)	*Japan*	*Total*
1961	7.3		10.2	17.5
1962	7.7		18.0	25.7
1963	6.9		31.6	38.5
1964	3.5	0.6	20.9	25.0
1965	7.6	2.7	9.8	20.1
1966	10.9	10.7	2.9	24.5
1967	—	14.3	3.3	—

Especially in the Bering Sea, the bulk of the landings until the last few years had been made by the Japanese fleet, which has achieved a maximum production of around 30.0 × 10³ tons. The resources are concentrated in a number of locations, among them the Pribiloff Islands in the Bering Sea. Here a Japanese fleet achieved the following production figures:

(tons × 10³)
1961—10.2
1962—21.0
1963—31.6
1964—20.9
1965— 8.8
1966— 2.9

This catastrophic collapse was probably due to gross overfishing, and the fleet has recently left these grounds, and turned its attention to the stocks of *P. goniurus* in the Anadyr Gulf.

There are extensive (but mostly unmeasured) areas in Alaskan coastal waters where shrimp fisheries may develop in the future. No reliable prediction of potential production is available. Now, fisheries are located on shrimp stocks with very high concentrations and/or close proximity to ports. As demand grows, operations will undoubtedly expand into more distant areas having lower shrimp densities. Among the potential shrimp areas are southeast Alaska and the Aleutian region. About 17,500 km^2 of ground near the Shumigan Islands can also be considered a potential shrimp area since the Soviet fishery there is now restricted to the offshore zone by US closure to foreign fishing of the 12 mi zone. Dominant species in unexploited areas are expected to be *Pandalus borealis* and *Pandalopsis dispar*.

It is probably a reasonable supposition that when all latent resources in this area (Bering Sea–Alaska) are in production the catches will be at least double the present figure. This is used for present purposes, and the total potential production is assumed to be about 100.0 × 10^3 tons per year.

Off Canada, the present trap and trawl fisheries are supported by: *Pandalus jordani*, *P. borealis*, *P. platyceros*, *P. hypsinotus*, *P. danae* and *Pandalopsis dispar*. Recent years' catches follow:

(tons × 10^3)	
1961—0.5	1964—0.5
1962—0.7	1965—0.8
1963—0.8	1966—0.8

Only the area of shrimp trawling grounds is known with any certainty, the total area trawled now and in the past being about 180 km^2. The area of trap grounds for *P. platyceros* appears to be considerably less. The prevailing rate of exploitation is high on trawling grounds near Vancouver and around Vancouver Island, for *P. borealis* and *P. jordani*, and greater effort there will not increase catches appreciably. Stocks of *P. platyceros* available for trapping are believed to be utilized at a low level.

Exploratory fishing between 1953 and 1967 has revealed unexploited grounds for *Pandalus borealis*, *P. jordani*, *P. platyceros*, and *Pandalopsis dispar*. Catch rates, using 70 ft semi-baloon Gulf, and 36 ft shrimp otter trawls, were from 20–380 kg per hour in inlets and 50–600 kg per hour on the outer coast. An estimate of potential trawling area is 630 km^2, and virtually all suitable shrimp trawling grounds have been explored, they are not now under exploitation. On the other hand, probably more than half the British Columbia coast remains to be explored by traps. Consideration of the known potential and hypothetically fishable grounds leads one to anticipate that production will increase by 450 tons within 10 years, giving a total production potential of about 12.0 × 10^3 tons annually.

On the open Washington coast *Pandalus jordani* supports a trawl fishery. The present annual catch is variable, ranging from nil to 2.5 × 10^3 tons annually, and about 0.4 × 10^3 tons were landed in 1967. The size of the fishery is determined by the strength of the dominant year-class, and it is believed that production is near the maximum sustainable yield. In years of high availability, boats which normally trawl for bottom fish convert to shrimp trawling.

No potential or hypothetical fishery off Washington is known.

Species under exploitation in Puget Sound include *Pandalus jordani*, *P. borealis*, *P. platyceros*, and *P. danae*. Annual catches for the area, including Hood Canal, in 1965 and 1966 were 28 and 22 tons, respectively. A breakdown of the 1967 commercial catch showed that traps took 8.3 tons and beam trawls 3 tons. Also in 1967 the catch of the sport trap fishery for *P. platyceros*, *P. danae*, and possibly *P. jordani*, was estimated at 8.6 tons. Stocks are presently being fished to near their maximum potential.

The potential production of *P. jordani* and *P. borealis* in South Puget Sound and Hood Canal, from about 400 km^2, is estimated at about 2.5 tons. Undoubtedly there are small isolated populations of shrimp scattered throughout Puget Sound which are not now being fished. The total potential for Washington is less than 3.0 × 10^3 tons annually.

The only species currently subjected to trawling off Oregon is *Pandalus jordani*. Production averaged 1.1 × 10^3 tons for the 10-year period ending in 1966, and a record of 4.7 × 10^3 tons was reached in 1967. Recent surveys of Oregon shrimp grounds have shown stocks to be abundant in most areas. Population size is known to vary from year to year, yet it appears that the exploitation rate is at a level somewhat below the optimum. Thus, an increase in production may be expected and it is anticipated that the catch will double within 10 years.

No potential shrimp trawl fisheries are known, or anticipated, off Oregon. Of a hypothetical nature is a trap fishery for *Pandalus platyceros* on the rocky bottom of Hecete Bank, Stonewall Bank, and Astoria Canyon, consisting of at least 450 km^2. This type of bottom appears similar to that elsewhere where *P. platyceros* is fished.

A total production potential of 10.0 × 10^3 tons may, therefore, be assumed for Oregon.

Shrimps being fished at present on the California coast are *Pandalus jordani* and *P. platyceros*. Trawl catches of the former species in recent years were:

(tons × 10^3)	
1962—0.8	1965—0.6
1963—0.9	1966—0.5
1964—0.4	1967—0.6

P. platyceros catches from a trap fishery are negligible, not reaching tens of tons in recent years.

Other minor fisheries for three species of *Crangon* exist in San Francisco Bay, and a potential exists for development of a small trawl fishery for *Sicyonia ingentis* off Santa Barbara.

It is unlikely that the total California potential production will be greater than 2.0 × 10^3 tons annually, even with all minor potential species in production.

C. *Spiny lobster resources*

A very small fishery, landing about 250 tons annually, occurs for *Panulirus interruptus* off Southern California. This is fully exploited and is negligible in the present context.

D. *Total production potential of Region IV*

The Table on p. 217 indicates the conservative estimates of potential production of crustacea from Region IV that have been used in the above discussions. This may very well be considerably too low, but there do not appear to be good reasons from presently available data to set it higher.

	Present	Potential
	(tons 10^3)	
Crabs		
Paralithodes camtschatica	150.0	100.0
Chionoecetes spp.	38.0	100.0
Cancer magister	$\approx$20.0	50.0
	(208.0)	(250.0)
Prawns		
Pandalus spp.		
Korea	5.0	5.0
Okhotsk Sea	?	10.0
Bering Sea and Gulf of Alaska	26.9	100.0
Canada	0.8	1.2
USA	8.4	15.0
	(41.1)	(131.2)
Total	249.1	381.2

Region V—Western Central Atlantic

This region comprises the Atlantic coast of the United States, the Gulf of Mexico, the Antilles and the Caribbean Sea, and south along the east coast of South America to the eastern boundary of Venezuela. This is an oceanographically complex region, covering the tropical and subtropical regions of the western Atlantic Ocean. The occurrence of great river effluents in the Gulf of Mexico, and along the coast of South America, combined with the occurrence of very extensive coastal lagoon systems renders it a very productive region for penaeid prawns, and these resources are perhaps more fully exploited here than anywhere else in the world mainly because of their proximity to the great crustacean markets of North America.

A. *Lobster resources*

Two species of spiny lobster occur in this region, both of them ranging rather widely from Bermuda, through the Gulf of Mexico and the Caribbean area, to the Atlantic coast of South America; these are *Panulirus argus* and *P. laevicauda*. The common lobster *Homarus americanus* has in recent years been trawled in deep water off Virginia and North Carolina, production reaching 75 tons annually.

The landings of these two species are partitioned between five countries as tabulated below:

REGIONAL LANDINGS OF SPINY LOBSTERS (tons 10^3)

Country	*1961*	*1962*	*1963*	*1964*	*1965*
Bahamas	—	—	—	—	1.2
Cuba	8.2	7.5	7.4	6.6	9.1
Mexico	—	—	0.2	0.2	0.1
USA	1.3	1.4	1.4	1.6	2.8
Venezuela	0.1	0.1	0.1	0.2	0.1
Total	9.6	9.0	9.1	8.0	13.3

Production from this region is now approaching 14.0×10^3 tons annually and although some areas, as around Cuba and Florida, the stocks are probably rather heavily exploited, it is reasonable to suppose that further development of the fishery is possible in the other relatively under-developed Antillean islands, and it is, therefore, guessed that a 50% increase over present production is likely to be possible. The potential of this region is, therefore, for present purposes, set at 21.0×10^3 tons annually. It is to be expected that the greatest increase in production will come from the islands of Jamaica, Dominica, and the Virgin Islands, with perhaps some new production from the eastern coast of Central America.

B. *Crab resources*

The greatest production of crabs in this region comes from the blue swimming crab and the Atlantic and Gulf coasts of the USA, *Callinectes sapidus*. The production from this fishery is considerably higher on the Atlantic than the Gulf coast of the USA but appears to have reached a point near its maximum sustainable production. The rather stable production in the last 5 years is probably due to a combination of resource limitation, and to the fact that the relatively low-priced products from this fishery still demand relatively high labour costs, and for this reason the northern fisheries of the Atlantic coast are declining relative to the remainder. The USA catches in recent years are as tabulated below:

US LANDINGS OF BLUE CRAB (*Callinectes sapidus*)
(tons × 10^3)

1961—69.3
1962—70.4
1963—65.9
1964—71.3
1965—75.9
1966—71.9 (Atlantic, 58.0 Gulf, 13.9)

A small number of other species of crabs are also exploited in the USA and the rest of the region, these in recent years obtaining a production rate of only about 2.0×10^3 tons a year. The statistical category "various crustacea" reaches 5.0 to 6.0×10^3 tons annually in the region as a whole and probably contains a rather large percentage of crabs of various species, probably dominated by swimming crabs throughout the Caribbean and Central America. The potential of crabs from the region is extremely difficult to guess and for present purposes is set at the extremely conservative level of 80.0×10^3 tons annually, which is very little in excess of the present blue crab production off the USA. It may very well be that this figure should rather have been set, and will prove in the long run to be 150.0×10^3 tons annually in view of recent (1968) indications on increased production on the Texas coast.

C. *Prawn resources*

It is these which are the most valuable and largest crustacean resources of the region and this is one of the major centres of prawn production of the world. Approximately 10 taxa of shrimps and prawns are currently exploited and of these 7 are shallow-living members of the genus *Penaeus*, the adults of which live upon the continental shelf, spawn there, and as far as it known pass their juvenile period in coastal lagoons. Two species of penaeids not of this genus and smaller in size having a shallow continental shelf ecology but without entering lagoons in the juvenile stage are also exploited, as is a single species of deep-living penaeid which occurs throughout the entire region on the upper parts of the continental slope. The exploited species with their scientific and industrial names and indication of their ranges within the region are given in the following tabulation:

Penaeus setiferus—white shrimp—New York to Campeche, Mexico
P. schmitti—camarón blanco—Honduras to Brazil
P. aztecus aztecus—brown shrimp—Massachusetts to Campeche
P. aztecus subtilis—camarón marrón—Honduras to Brazil
P. duorarum duorarum—pink shrimp—Chesapeake Bay to Mexico
P. d. notialis—caramel shrimp—Cuba to Brazil
P. brasiliensis—spotted pink shrimp—disjunct, Carolinas to Brazil
Xiphopeneus kroyeri—seabob—North Carolina to Brazil
Sicyonia brevirostris—rock shrimp—Virginia to Yucatan
Hymenopenaeus robustus—royal red shrimp—entire region

The white shrimp, *Penaeus setiferus*, has three centres of abundance where it is presently fished intensively. These are (1) off Georgia and north-eastern Florida on the Atlantic coast of the USA, (2) off the coast of Louisiana on the Gulf coast of the USA, and (3) near Isla del Carmen, Campeche, on the eastern coast of Mexico.

The camarón blanco, *P. schmitti*, is more dispersed than the above species, and fishable concentrations occur especially off Cuba, off the Honduras–Nicaragua area, and off Venezuela, but in none of these places do stocks appear to be comparable in density to those of *P. setiferus* off Louisiana.

P. aztecus aztecus, the brown shrimp, occurs in four principal fishable concentrations: on the Atlantic coast of the USA off the Carolinas; in the Gulf of Mexico between the Mississippi and north-eastern Mexico; from the north of Tampico to Veracruz, Mexico; and finally along the coast of Tabasco and south-western Campeche, Mexico. The area of greatest abundance is in the north-central and north-western Gulf of Mexico. The principal stocks of *P. a. subtilis* appear to be to the south of this region along the coasts of Guyana, Surinam, French Guiana, and Brazil, and this species is only of importance in Region V along the coast of Venezuela.

P. duorarum duorarum occurs in two great concentrations, one along the southwest coast of Florida and the other on the Campeche banks off the east coast of Mexico. *P. d. notialis* occurs in fishable concentrations only at Cuba, the Honduras–Nicaragua area, and in the Gulf of Venezuela.

P. brasiliensis is not a great commercial importance in this region, except in the region from Cabo Catoche to Isla Mujeres, Mexico, the coast of Honduras and Nicaragua, and to some extent to Colombia and Venezuela. The largest stocks are apparently to the south of the region.

Commercial concentrations of the seabob, *Xiphopeneus kroyeri*, occur as follows: in the northern Gulf of Mexico, particularly to the west of the mouth of the Mississippi River; off Nicaragua; of eastern Venezuela; and off Trinidad. The largest stocks of this species are also to the south of this region. Known concentrations of the rock shrimp, *Sicyonia brevirostris*, occur from about Charleston, South Carolina to New Smyrna, Florida; in the north-western Gulf of Mexico; and in the Gulf of Campeche.

The deep-water shrimp, *Hymenopenaeus robustus*, known to the trade as the royal red shrimp, is the only species of deep-water crustacean considered in this area, although a number of other species occur with a rather similar ecology. These are three localities where fishable concentrations of the royal red shrimp are known to exist. These are along the coast of the USA and are located (1) off the east coast of Florida between latitude 27–31°N, (2) along the Florida Straits between longitudes 82–84°W, and (3) southeast of the Mississippi River Delta between longitudes 87–91°W. These grounds are named, respectively, St. Augustine, Dry Tortugas, and Mississippi Delta.

In addition to these species which are discussed above, and on which the present production in the region is based, there are of course also many other species of prawns and shrimps in the area, these being mostly of small size (such as those of the genera *Parapenaeus*, *Penaeopsis*, and *Trachypeneus*) that may or may not be taken and utilized incidentally with present commercial operations, and which may or may not have future potential as a commercial resource. These have not been included either because they are not reported in present landings or because it is unlikely that specific fisheries will develop in the foreseeable future from them. Also not included in the present consideration are the deep-water penaeids (*Aristaeomorpha foliacea*, *Aristeus antennatus*, *Penaeopsis serrata*, and *Plesiopenaeus edwardsianus*), and the pandalid *Plesionika edwardsii* have been reported on numerous occasions as occurring throughout the area, but none of these except *Penaeopsis serrata* (which is of small size) has been located in concentrations sufficient to suggest supporting the commercial fishery. The following tabulation summarizes the present production of all species of prawn throughout the area by countries, and their estimated potential production. This cannot be broken down by species, as in almost every case the available national statistics are not stratified by species.

Country	*Present*	*Potential*
	(tons 10^3)	
USA	78.7	102.0–127.0
Cuba	2.0	2.5
Mexico	30.9	33.0
Bahamas	1.0	2.0
British Honduras	0.2	0.4
Guatemala	+	0.2
Honduras	2.1	3.0
Nicaragua	2.1	4.0
Costa Rica	+	0.2
Panama	+	0.2
Colombia	0.4	2.0
Venezuela	7.8	11.0
Total	125.0	160.0–185.0

The estimates of present production or current production in the above table have been derived by Lindner, not from single recent years data but rather from long-term averages. For instance, the US current production is derived from the 10-year average, 1958–67; the Mexican current production is based on the 9-year average, 1958–66 and includes landings of US vessels whose catches were made off the coast of Mexico. In some cases, such as that of Nicaragua, the estimates are rather made on the best available data even though this is for only a single year, in this case 1966, and from landings in that year by US vessels whose catches were reported as having been made off the coast of Nicaragua. The data from Venezuela and Mexico are probably not very reliable as a sizeable quantity of the landings in these areas are reported as "heads-on" in the data but in fact have probably been headed before landing; for these two countries, therefore, a factor of 1.68 to convert headless landings to live weight has been used. It was necessary to group all countries and entities throughout the Bahamas, the Greater and Lesser Antilles, with the exception of Cuba, for although practically all have small localized shrimp fisheries their magnitude is not large nor is it likely to become so, and available landing data are so scanty that both estimated production and potential production are really only guesses.

It should be noted that the estimates of potential landings given in the above tabulation include 15.0–40.0 tons from the US fishery which might be expected eventually to accrue by changing present management procedures. Eliminating this accrual from good management we arrive a little more than 140.0 × 10^3 tons as the potential we can expect by increased fishing in some localities and by fishing species which are not now utilized. In other words we can expect only about a 16% gain in landings by increasing our fishing effort. It would be quite unrealistic at the present moment to attempt to estimate what improved management procedures might accomplish in the remainder of the region and although these might significantly lift the final estimated potential production this is not done at the present as it would be entirely unrealistic.

D. *Total resource potential of Region V*

The estimates of present production and of potential production discussed above are tabulated below:

	Present (tons	*Potential* 10^3)
Lobsters		
Panulirus spp.	13.3	21.0
Crabs		
Callinectes spp.	74.9	80.0
Others	2.0	
Prawns		
Prawns and Crangonid prawns and shrimps	125.0	160.0
Total	215.2	261.0

The rather modest potential increase in production suggested for this region is undoubtedly a function of the relatively high level of exploitation already achieved, and which is discussed in the text above.

Region VI—Eastern Central Atlantic

Present catches are low, less than 5.0 × 10^3 tons; resources comprise crayfish of several species, less than 10 species of penaeid prawns, and a few other minor species. Deliberate exploration for crustaceans has been carried out only in the Bight of Biafra, and the unsatisfactory data for crustaceans from fish resource surveys make numerical projections of potential resources, and future yields very subjective.

A. *Lobster resource*

(i) *Palinurus mauritanicus*

Habitat: west coast of Africa from 18–25°N, 60–600 m, especially at 200 m on the Arguin Bank. *Actual landings:* 1963—2.5 × 10^3 tons from 40 French and Spanish vessels. *Potential:* presently over-fished (Postel 1967).

(ii) *Palinurus charlestoni*

Habitat: Cape Verde Islands, 150–300 m. *Actual landings:* 10–20 tons. *Potential:* perhaps 1,000 tons with other species (Postel 1967).

(iii) *Panulirus regius*

Habitat: from Cape Juby in Morocco to the south of Angola, including Cape Verde and Gulf of Guinea Islands; down to 40 m, but mostly <at 20 m, on rocky and other hard bottoms. *Actual landings:* 200–500 tons from Senegal–Mauritania directly to France; 75–125 tons at Dakar, Senegal; 10–50 tons in Ivory Coast; 10–20 tons in several other West African ports. *Potential:* negligible, perhaps 100 tons, in tropical Gulf of Guinea; 400 tons in Senegal and Mauritania; Angolan potential not known but possibly between 250–500 tons (Postel 1967, Williams 1968).

B. *Prawn resources*

(i) *Penaeus duorarum*

Habitat: in Eastern Atlantic the form commonly known under this name occurs from Cape Blanco to Angola; its identity with the Western Atlantic form does not appear to have been critically examined; coastal, down to 100 m, most common and abundant from 30–50 m in thermocline water and on soft mud associated with this depth. Juveniles in estuarine systems and lagoons. *Actual landings:* as tabulated below, in 1966, just under 3.5 × 10^3 tons for this region. *Potential:* only suggestion that MSY has presently been reached comes from Senegal rivers (e.g. R. Casamance). Elsewhere, exploitation is just starting, particularly from Nigerian ports, where production has now reached about 2.8 × 10^3 tons annually. Surveys, and patterns of exploitation, indicate that centres of production will be from Senegal to Guinea

PENAEUS DUORARUM, LANDINGS IN 1966 (tons × 10^3)

Senegal	—rivers	0.45
	—sea	0.52
Ivory Coast	—lagoons	0.30
	—sea	0.15
Dhomey	—lagoons	0.27
Nigeria	—sea	1.20
Cameroon	—sea	0.12
Gabon	—sea	[illegible]
Congo	—sea	[illegible]
Angola	—sea	0.15
Total		3.16

and from Dahomey to Gabon, including Fernando Po, with the greatest resources off the Niger Delta and in the Bight of Biafra. Catches off the US coast of the Gulf of Mexico of this and related species reaches 75.0 × 10³ tons per year and it seems not improbable that a figure similar to this, between 50.0 × 10³ tons and 100.0 × 10³ tons is likely for the Gulf of Guinea, and could even be surpassed; the lower figure is adopted for present purposes.

(ii) *Parapenaeopsis atlantica*

Habitat: from Senegal to Angola, coastal and down to 60 m, but most abundant at 10–40 m; juveniles do not enter estuaries and lagoons. *Actual landings:* statistically, not generally separated from those of *P. duorarum*, and only in Ivory Coast and Congo are data available: in the former from 15–30 tons, in the latter from 1–5 tons annually appear to be landed. *Potential:* limited, but specialized fisheries may develop, as for the "seabob" and other shrimps smaller than *P. duorarum* in the Gulf of Mexico. Impossible to quantify an estimate at this moment.

(iii) *Parapenaeus longirostris*

Habitat: Mediterranean and west coast of Africa south to Angola; in tropical region occurs on deeper parts of the shelf expecially between 150–300 m. *Actual landings:* negligible, less than 50 tons annually by a few Spanish vessels north of Cape Verde. *Potential:* although survey data indicate the presence of this species throughout the Gulf of Guinea, it is not presently possible to quantify the potential yield (Crosnier 1967, Monod 1967, Williams 1968).

(iv) *Plesiopenaeus edwardsianus; Plesionika martia; Aristeus varideus; A. antennatus; Glyphus marsupialis*

Habitat: these are the main elements of a shrimp fauna on the upper part of the continental slope which occurs probably throughout the inter-tropical region from 200–900 m, each species probably having a preferred depth range. *Actual landings:* unknown, but some exploitation by Spanish trawlers off Sierra Leone and Senegal, landing in Las Palmas and Huelva. *Potential:* unquantifiable, but by analogy with Mediterranean fishery for some of these, and other related species with similar ecology, a yield of 10.0 × 10³ tons annually in the tropical zone could be postulated (Crosnier 1967, Massuti MS., Monod 1967, Ivanov 1964, Williams 1968).

(v) *Palaemon hastatus; Hippolysmata hastatoides*

Habitat: estuaries and lagoons of tropical region, coming onto shelf areas during rainy season. Very shallow, along beaches. *Actual landings:* not known, but probably running into some hundreds of tons since beach seine catches at Lagos may take more than half-a-ton per haul during the season. *Potential:* unquantifiable, but probably less than 1,000 tons for the whole Gulf.

C. *Crab resources*

(i) *Portunus validus; Callinectes* spp.

Habitat: blue swimming crabs are common and abundant throughout the Gulf of Guinea, coastal and estuarine out to 50 m, usually shallower. *Portunus* dominant on continental shelf, *Callinectes* spp. in estuaries and lagoons. *Actual landings:* presently not quantified, and negligible except as minor element in indigenous fisheries. Trawler catches mostly discarded. *Potential:* by analogy with swimming crab fishery on eastern coast of USA, a yield of 10.0 × 10³ tons for Gulf of Guinea appears possible, providing an economic basis was established. It seems extremely improbable that this potential will be realized in the foreseeable future, however.

D. *Total potential resources of Region VI*

The following tabulation is based on the production and potential estimates made above:

	Present	*Potential*
	(tons × 10³)	
Lobsters		
Palinurus mauritanicus	2.5	2.0
P. charlestoni	+	1.0
P. regius	+	1.0
	(2.5)	(4.0)
Crabs		
Portunus validus	+	10.0
		(10.0)
Prawns		
Penaeus duorarum	4.6	50.0
Parapenaeopsis atlantica	+	1.0
Parapenaeus longirostris	+	1.0
Deep penaeds	+	10.0
Palaemon hastatus *Hippolysmata hastatoides*	+	1.0
	(4.6)	(63.0)
Total	>6.0	77.0

That the suggested increase in production for this region is relatively large is a reflection of the fact that it is only in the last few years that exploitation of the most important crustacean resources, those of *Penaeus duorarum*, has been started. In the present state of knowledge of the stocks of this species the suggestion made here as to potential production must be extremely subjective.

Region VII—Western Indian Ocean

This region extends northwards from the boundary between South Africa and Mozambique along the coast of east Africa and around the Arabian Sea up to the western coast of Ceylon. It is one of the larger and more diverse regions and contains a very high number of species of crustacea, some of which support important fisheries.

A. *Rock Lobster resources*

There appear to be no major resources, or centres of production, of rock lobsters in this region which is to the north of the important stocks of *Jasus lalandii* in southern Africa. Only around the Kerguelen Island in the extreme southern part of this region is there a rock lobster resource of any abundance, and this is neither very extensive, nor are there good production figures for it, but it is known to be exploited by French langouste boats, and the species which is exploited there and in small amounts round New Amsterdam and St. Paul Islands is believed to be *Jasus paulensis*.

Turning to the African coast, the Natal rock lobster *Palinurus gilchristi* extends northwards along the southern coast of Mozambique, where small quantities are taken off South Africa. The exploitation of this species is just beginning and a plant capable of freezing 2.5×10^3 tons annually has been installed in Lourenço Marques. This figure is here used as the potential for *P. gilchristi* from Natal and Mozambique. In the Mozambique Channel, *Panulirus ornatus*, *P. longipes* and *P. versicolor* are taken by a number of methods and produce approximately 150 tons annually. From the nature of the environment, and the distribution of these species, it is impossible to employ industrial methods of fishing, and the production of these species in this area will be determined by the amount of individual effort which local fishermen are prepared to put into the fishery. Postel suggests a total production of 600–700 tons from this area annually.

On the southeast coast of Madagascar, *P. homarus* and *P. penicillatus* are taken with nets; the rate of production is extremely low, of the order of 20 tons annually. In the Mascarene Islands, *P. penicillatus*, *P. ornatus* and *P. longipes* are taken in small quantities along the coral reefs by local divers. In the Red Sea and the Gulf of Aden, *P. penicillatus* and *P. ornatus* are again present, and are taken in very small quantities by local divers.

Recently promising catches of deep-sea lobster, *Puerulus sewelli* have been taken in deep water (100–150 fm, *c.* 200–300 m) off Cochin.

In sum, it appears unlikely that the production of spiny lobsters throughout the region will significantly exceed 3.0×10^3 tons annually.

B. *Crab resources*

It is presently impossible to estimate the catches of crabs from this region. The rather large quantities of "other crustacea" reported in the landing statistics of India and Pakistan suggest that significant quantities of crabs, probably mostly portunid swimming crabs, are produced but the present breakdown in statistics makes it impossible to define this.

The only studies of edible crabs in the Indian Ocean, from a commercial point of view, appears to be that of Guinot (1967a). The degree to which crabs are utilized in the Indian Ocean appears to vary very widely, especially for smaller species, and the potential yield from more widespread fishing than is practised at the moment could be quite high, although Guinot attempts no estimates of production rates. He implies that at least some species, for example *Portunus pelagicus*, are rather heavily fished.

Off Mozambique, several species of crabs are landed in small quantities, partly as a by-product of the shrimp fishery. They include *Schylla serrata*, *Portunus pelagica*, and *P. sanguinolenta*. Possibly appreciable stocks of *S. serrata* (mangrove crab) occur in mangrove swamps along the entire East African coast.

C. *Shrimp and prawn resources*

In Mozambique, just to the north of the South African border, the important species appear to be *Penaeus indicus*, *P. monodon*, *P. semisulcatus*, and *Metapenaeus monoceros*. *P. indicus* constitutes about 70% of the catches. Species of secondary importance are *P. japonicus* and *P. latisulcatus*. The annual production in 1,000 metric tons of these species on the coast of Mozambique is given in the following tabulation; this production comes from an area of about 3,000 km² of offshore trawling grounds and 1,000 km² of inshore bays and estuaries, of which the inshore areas of Delagoa Bay, Inhambane, the mouth of the Save River and Mecufi are the most important.

	1964	*1965*	*1966*
Offshore trawling	—	0.1	0.1
Inshore fisheries (beach seines and traps)	0.4	0.4	0.6
Total	0.4	0.5	0.7

It is thought that commercially exploitable stocks of *Hymenopenaeus triarthrus* are present in deeper water off Mozambique, below about 200 fm, together with species of *Aristeus* and *Hemipenaeus* which might contribute to this potential fishery. It seems likely that future production may expand in the shallow areas to the north and south of the Limpopo River, along the sofala Bank as far north as the Zambesi River mouth; in deeper water, at a depth of around 250 fm, prawns are abundant from Moma to Mozambique Island.

No detailed data are available for the fisheries off Madagascar which are based largely on stake traps and are much diffused, but statistics are maintained by one firm which took 30 tons from 20 traps during 1959; FAO statistics indicate 1.3×10^3 tons in 1966 and this number seems reasonable. *Penaeus indicus* probably constitutes about 70% of the catches, *P. monodon* 15% and *Metapenaeus monoceros* a further 15%; *Penaeus japonicus* and *Trachypenaeus curvirostris* may be common at times but are never caught in large quantities by present methods. Some shrimp trawlers may have recently begun operations but no details are available of their landings. A small fishery for *Nephrops andamanicus* has recently developed.

There are no good statistical data for present prawn and shrimp production from Tanzania though the FAO statistics mention a production rate of 0.5×10^3 tons annually. It is known that small Japanese-operated trawlers have been exploring the coast, and recently have been reported to be taking 10 tons per day from the region north of Dar-es-Salaam. It is likely from survey work in this area that the species which they are taking are primarily *Penaeus monodon*, *P. semisulcatus* and *P. indicus*. There are small subsistence level fisheries using fixed traps in the Rufiji Delta where small quantities of large *P. monodon* and all sizes of *P. indicus* together with small quantities of *Metapenaeus* spp. constitute the catches. On the coast of Kenya, small boat operations in the extreme south (Shimoni), and in the extreme north (Lamu) have been building up over the last 18 months but there is no record of their catch rate, nor of the species involved; it is considered likely, however, that the catch composition will not differ very much from that of Tanzania. There is no knowledge of prawn resources off the coast of Somalia, and there appears to be no fishery in that area. An annual spawning run of penaeid shrimps in the mouth of the Juba River has been recorded, and small numbers of penaeids are known to occur in the estuaries of other small rivers but these stocks have neither been quantified nor exploited.

In the Red Sea, the Gulf of Aden and off the southern Arabian Peninsula there are fisheries for *Penaeus semisulcatus, P. japonicus, P. latisulcatus, Metapenaeus monoceros, M. stebbingi*, and *Trachypenaeus curvirostris*, but only *P. semisulcatus* is likely to be important commercially. The only statistical data from this area are those from Egypt which in 1963 quoted a total shrimp and prawn catch of 10.4 × 10^3 tons but without any record of how much, if any, of this catch was taken from the Red Sea, or the Gulf of Aden. A very small seasonal cast-net fishery for prawns exists in Aden at the inlets to the salt pans.

In the Persian and Arabian Gulfs an important prawn fishery has grown up in recent years, in which *Penaeus semisulcatus* dominates the catches and which also include small quantities of *P. latisulcatus* and *Metapenaeus affinis*, except for the Hormuz Strait-Bandar Abbas region where *Penaeus merguiensis* may be the dominant species in the catches. The estimated total commercial catches from this area in recent years are tabulated below.

(tons × 10^3)

1959—0.6
1960—1.1
1961—1.7
1962—0.9
1963—3.1
1964—5.8
1965—11.4
1966—16.1
1967—14.6

The total area of the Gulf off Iran, Iraq, Kuwait, etc. is about 239.0 × 10^3 km^2: of this total about 142.8 × 10^3 km^2 is shallower than 20 fm (*c*. 36 m). The exploitable area of the Gulf is so limited by sand banks and coral reefs along the Arabian side, and by soft mud in waters deeper than about 25 fm (*c*. 45 m), that only 10–20% of the total area may be trawlable, say 35.0 × 10^3 km^2.

In the past 2 years, 1966 and 1967, the catch per unit of effort has declined and in 1967 the total production also fell though it increased again in 1968. Some concern has been expressed for the stocks, but a very recent assessment has concluded that there is no clear evidence as yet that the decrease in total catch was due to fishing pressure either directly or indirectly. It has been acknowledged, however, that in the more heavily-fished areas a further increase in fishing effort might reduce the total catch. In view of the present status of the stocks, it would be unrealistic to expect any further considerable expansion of the fishery, although some further developments in the more lightly fished areas is possible, and a maximum sustained production rate of 15.0 × 10^3 tons is used here for these Gulfs.

Off West Pakistan, *Penaeus merguiensis* is recorded as outnumbering all other prawn species in catches from coastal waters, with *Penaeus semisulcatus, P. penicillatus, Metapenaeus monoceros*, and *Parapenaeopsis stylifera* also being important. Caridean species do not appear to be important. The total production of shrimps and prawns from these resources in the last few years is as follows:

(tons × 10^3)

1961— 6.6
1962— 4.6
1963— 9.2
1964—16.1
1965—18.0
1966—18.2
1967—17.2
1968—15.5

Commercial fishing by shrimp trawlers is conducted in the 7–23 m depth zone along the 300 ml of this coast of Pakistan, and by beach seines in the creeks. The total fishing area is about 11.0 × 10^3 km^2. The catch statistics show a stabilization of catch since 1964 despite an increase in the number of boats from 226 in 1964 to 363 in 1968. Most of the fishing is concentrated within about 50 mi of Karachi. These grounds are probably fully exploited, but exploratory fishing has shown that good catches can be obtained on most distant grounds, especially south of the Indus. These grounds do not seem to be heavily exploited and the shrimp there are noticeably bigger. A sustained yield of 25.0 × 10^3 tons should be possible with a more rational distribution of fishing.

The present fisheries along the west coast of India are rather heterogeneous in their specific composition, and productivity varies markedly along the coast. On the northwest coast (Maharashtra and Gujerat) which produces over 50% of the catch, the prawns are rather small species, being dominated by *Metapenaeus affinis, Parapenaeopsis hardwickii, P. stylifera* and *Solenocera indica*. The dominant caridean species are *Palaemon tenuipes* and *Hippolysmata ensirostris*, and these are caught in enormous numbers, together with the sergestid *Acetes indicus*, from April–May and from November–December. The fishing techniques for all these species are fixed bag and stake nets.

Along the south-western coast of India there is a bigger variety of fishing gear used and the catch is distributed in the approximate proportions 3:3:2:sea (trawls, boat-seines):backwaters (stake nets, dipnets, cast nets):paddy fields. The most important species are *Penaeus indicus, Metapenaeus dobsoni, M. affinis* and *M. monoceros* (marine and backwaters), *Parapenaeopsis stylifera* (only at sea), and *Macrobrachium rosenbergii* (only riverine). The purely fresh-water species are of small importance and *M. rosenbergii* is caught in very limited quantities in certain areas only. The production from the Indian west coast of penaeids and caridean prawns in recent years is tabulated below:

Year	*Penaeid*	*Caridean* (tons × 10^3)	*Total*
1960*	27.5	35.0	62.5
1961*	32.9	22.0	54.9
1962*	42.2	34.6	76.8
1963*	30.7	39.5	70.3
1964*	52.0	30.2	82.2
1965†	28.0	41.0	69.0
1966†	45.7	34.7	80.4

* Data from Indian Fisheries Department
† Data from FAO

The littoral prawns which are currently exploited occur down to about 30 m along the west coast of India but all the best areas are inside the 35 m line. Survey fishing in the 100–200 fm (180–360 m) range shows fairly large numbers of *Penaeopsis rectacuta* and *Aristeus* *semidentatus*, but there is no estimate of the likely production from these deep water resources. From the manner in which the production has been rising in the last 5 years and from the fact that no production has yet been made from deep water resources it is considered for present purposes that a 20% increase over present production is quite likely, and a total production of 100.0 × 10^3 tons for the total west coast of India catch in the future years is, therefore, assumed.

Thirty-one species of penaeid prawn have been recorded from the waters of Ceylon. No analysis of the specific composition of prawn catches has been undertaken but the following species have been classified as being abundant on the west coast: *Penaeus indicus*, *P. merguiensis*, *P. semisulcatus*, *Metapenaeus dobsoni* (most abundant of all penaeids, but small in size), *Trachypenaeus salaco*, and *Parapenaeopsis coromandelica.* Only the first three of these species are likely to be of major commercial importance, and caridean prawns are of negligible importance. The catch in 1965 was 770 metric tons from Ceylon and it does not appear that the catches have yet passed the level of 1.0 × 10^3 tons annually which is suggested here as the potential production from the west coast of Ceylon.

The prawn catches in the Western Indian Ocean may be summarized as follows: *Penaeus indicus*, one of the species in which the juvenile passes a part of its life in a fresh or brackish water environment is the dominant prawn along most of the southern part of the East African coastline, and of Madagascar. Further northward (with increasingly arid terrestrial conditions) the dominant species are those which are less dependent on fresh-water habitats, such as *P. semisulcatus* and *P. merguiensis*, although post-larvae of both these species will migrate into fresh or brackish water areas if they can. These three species may all grow to a good size. The west coast of India has a much more varied penaeid fauna than do the regions to the west, and some elements are rather small in individual size; it is difficult to be certain which are the most important species in the absence of objective data, but further to the south, off Ceylon, all three of those mentioned above are important in the catches.

Wherever it is taken, namely throughout the region excepting the Red Sea, *Penaeus monodon* usually makes an important element of the catches, not because it is abundant but because of its very large adult size and excellent price in the market.

D. *Total resource potential of Region VII*

From calculations based upon the catch per km² per year over various prawning grounds in the Western Indian Ocean and on the assumed total area of hypothetical prawning grounds, Hall suggests that the total potential production of penaeids in the Western Indian Ocean might be approximately twice the present level and the production of caridean shrimps would be additional to this. This would give a total production of at least 200.0 × 10^3 tons annually and this is used as the regional potential for present purposes even though it is not supported in detail in the following tabulation of present and potential production in Region VII.

	*Present**	*Potential†*
	(tons × 10^3)	
Spiny lobsters		
Africa	<0.3	3.0
Madagascar	<0.1	<0.1
	(0.4)	(3.1)
Penaeid prawns		
Mozambique	0.7	1.0
Tanzania	0.1	0.5
Kenya	0.1	0.5
Red Sea, etc.	5.0	5.0
Persian Gulf, etc.	16.1	20.0
West Pakistan	18.2	25.0
India, west coast	45.7	50.0
Ceylon, west coast	0.8	1.0
Madagascar	1.3	1.3
	(86.6)	(104.3)
Caridean shrimps		
India, west coast	34.7	40.0(?)
	(34.7)	(40.0)
Total	121.7	147.4 (= 200.0, Hall)

* Data from most recent available year.

† Because of lack of data on present production a potential has not been guessed for portunid crabs, but this may be large.

Region VIII—Eastern Indian Ocean

This region extends from the east coast of Ceylon, around the Bay of Bengal and includes, at its extreme southeast corner, the western coast of Australia, the Indian Ocean coasts of Sumatra and Java, and the west coast of Malaya and Thailand.

A. *Spiny lobster resources*

The only part of this region for which there are data on the occurrence of spiny lobsters and on the production of fisheries for them is Western Australia. Several species occur here but only one, *Panulirus longipes cygnus* supports the important fishery. This species occurs from 21°–34°S along the west coast of Australia, the majority of the commercial catch being taken from 28°–32°S, the crayfish boats operating from a number of ports between Fremantle and Geraldton. Fishing grounds are approximately 24.0 × 10^3 km² of water shallower than 155 m, though not all of this areas has substrate suitable for this species. During the "red crayfish season", the boats may operate from offshore islands such as the Houtman Abrolhos Islands. The fishing season extends from late spring through to the next southern winter and catch data are, therefore, given for pairs of years. The production for recent seasons follows:

(tons × 10^3)

1958–59—8.0
1959–60—8.8
1960–61—8.2
1961–62—8.7
1962–63—9.1

1963–64—8.1
1964–65—7.4
1965–66—8.0
1966–67—8.6
1967–68—9.9

A sustainable level of catch of 8 ± 1 × 10^3 tons per year has been suggested (Bowen and Chittleborough 1966, Sheard 1962). Present exploitation rates are high (exceeding 60%).

The southern crayfish (*Jasus novaehollandiae*) is common on the coast to the south of 33°S, but surveys have failed to find sufficient to support a fishery in this region.

On the western coast of Australia north of 22°S, several species of panulirids occur (*P. versicolor*, *P. penicillatus*, *P. ornatus* and *P. polyphagus*). Local areas of abundance have been claimed for certain of these, but test fishing failed to obtain any catch although various types of traps and bait were used. The potential resource of these species is not known, but it is not considered to be high in this region.

B. *Crab resources*

Crabs are taken in small quantities in Western Australia and throughout the region. The same remarks as were made for Region VII apply also to this region in regard to this resource, which is presently unquantifiable.

C. *Shrimp and prawn resources*

The catch of prawns along the east coast of Ceylon in 1965 amounted to 1.5 × 10³ tons; no analysis of the specific composition of the catches has been made, but the following species have been recorded as being abundant: *Penaeus indicus*, *P. merguiensis*, *P. semisulcatus*, *Metapenaeus affinis*, *M. ensis*, *M. dobsoni* (most abundant of all penaeids, but rather small in size), *M. elegans*, *Metapenaeopsis stridulans*, *M. toloensis*, *Trachypeneus salaco*, *Atypopeneus stendodactylus*. The first three of these species are undoubtedly of the greatest importance but the others, excluding *T. salaco*, may be abundant locally. Caridean species are of negligible importance in this area.

There are not data available on the status of the exploited stocks, but the 1965 catch apparently came entirely from the 0–20 fm range, so the deeper resources at the edge of the continental shelf which may be assumed to exist have neither been surveyed, nor are in production.

The prawn fisheries along the east coast of India amount to 10.0 to 12.0 × 10³ tons annually; the most important species are *Penaeus indicus*, *P. monodon*, *P. semisulcatus*, *Metapenaeus dobsoni*, *M. affinis*, *M. brevicornis* and the caridean species *Palaemon styliferus*. There are four areas within which the resources are most abundant: (a) rivers and other entirely freshwater areas, dominated by species of *Palaemon* and *Macrobranchium*, of which *M. rosenbergii* is the largest, although *P. styliferus* dominates the riverine catches numerically; (b) the Chilka, Kolleru and Pulicat Lakes, which are major coastal lagoons, and which produce more than 1.0 × 10³ tons annually from small locally-made shrimp traps. *P. indicus* constitutes some 65% of these catches, with *P. monodon* and *Metapenaeus monoceros* contributing about 15% each; (c) the deltaic areas of the River Ganges which also produce about 1.0 × 10³ tons annually and where *Metapenaeus brevicornis*, *Parapenaeopsis*, *sculptilis*, *Palaemon styleriferus* and *Acetes indicus* are the most important species; (d) offshore areas accounting for most of the balance of the prawn catches, and producing almost 10.0 × 10³ tons annually. The catches of the Andaman and Laccadive Islands are not included in these statistics, nor in those tabulated below, and are less than 5 metric tons annually. The total catches from the above four areas during recent years are tabulated.

Year	*Penaeid*	*Caridean* (tons × 10³)	*Total*
1960*	4.3	1.3	5.5
1961*	6.2	1.7	7.9
1962*	6.0	0.4	6.4
1963*	10.3	1.0	11.3
1964*	11.4	1.3	12.7
1965†	7.9	0.4	8.3
1966†	9.8	0.7	10.5

* Data from Indian Fisheries Department
† Data from FAO

Again, as for the coast of Ceylon, the entire production from the Indian sector of the Bay of Bengal is from shallow water from 0-20 fm and does not include any production from such deeper resources at the edge of the continental shelf and below as may be assumed to exist.

Along the coast of East Pakistan, a fishery for palaemonid species flourishes during the rainy season when the salinity of the coastal waters is lowered by the rains, but during the remainder of the year the catches are dominated by penaeids, among which the most abundant appear to be *Penaeus semisulcatus*, referred to as the most important in the deltaic region and *P. indicus* and *Parapenaeopsis sculptilis*.

Commercial fishing is currently carried out entirely in estuarine areas, and has hardly expanded yet onto the continental shelf and certainly no catches are produced from the deeper resources which presumably exist in the Bay of Bengal.

There are no published data on the prawn and shrimp fishery of Burma, since the statements that the 1953 to 1954 season's catch from the floating prawn traps in the deltaic area took approximately 5.0 × 10³ metric tons. There are certaintly very extensive unexploited resources in the shallow continental shelf area but these are apparently unknown at present, although Hall suggests that the Gulf of Martaban (which exceeds 35.0 × 10³ km² in area) may be particularly valuable.

There are no good data on the prawn fisheries from the west coast of Thailand, for it is not possible to separate the catches from the east and west coasts in the fishery statistics from this country, which show that the total catch of marine and estuarine prawns in 1966 was 45.3 × 10³ tons. It is considered however that the bulk of these catches came from the east side of the peninsula (see Region IX), and based on the relative length of the coastlines, the distribution of the human populations, and the location of major rivers, Hall suggests that possibly 10% of the catch may be associated with the Indian Ocean, e.g. marine and estuarine—4.5 × 10³ tons; freshwater—0.3 × 10³ tons.

By comparison with the specific composition of catches from Penang and the Alor Star area of northern Malaysia it is probably that the dominant marine species on the west coast of Thailand are *Parapenaeopsis harwickii*, *P. hungerfordi*, *P. sculptilis*, *P. coromandelica*, *Penaeus merguiensis*, *Metapenaeus brevicornis* and *M. affinis*. In the mangrove areas with a fresh or brackish environment the dominant species are likely to be *Penaeus indicus*, and *Metapenaeus ensis*.

There is no recent information on the Indonesian prawn fishery which will enable us to separate the catch along the Indian Ocean coast of Sumatra and Java from that along their northern coast; but, bearing in mind the steepness of the Indian Ocean coastline profile of these islands compared with the Strait of Malacca/Java Sea profile, and the concentration of populations on the side away from the Indian Ocean, possibly 5% of the catch should be attributed to the Indian Ocean. Hall suggests that this is a total of a little less than 1.0×10^3 tons annually. The catches from Indonesia, like those from India, consist of four fairly distinct elements: (a) the marine catch taken by trawling, (b) the penaeid catch taken from prawn ponds, of which the most important species are *Penaeus indicus*, *P. semisulcatus* which is appreciated for its large size, *Metapenaeus ensis* and *M. brevicornis*, (c) the non-penaeid shrimp catch consisting mostly of fairly large freshwater species of which *Macrobrachium rosenbergii* is the most appreciated and very widely distributed. Other species quoted are *M. equidens*, *M. pilimanus*, *M. sintangense* and *M. lar*, (d) the non-penaeid catch consisting mainly of small atyids and Caridina species, but including also mysids and possibly *Acetes* spp., the importance of which lies in their vast numbers of small individuals.

Along the west coast of Malaysia the fishery for Udang prawns, or large penaeids, is not detailed statistically but in the south the important species are probably the same as those at Singapore, with the following being the most abundant: *Metapenaeus ensis*; *Penaeus indicus*; *Metapenaeus burkenroadi* and *affinis*. Local variations occur, so that inshore Malacca catches have *M. affinis* as a major element while *Penaeus merguiensis* is important in the northwest of Malaysia, where inshore fisheries tend to de dominated by *Parapenaeopsis* species, especially *P. hardwickii* and sometimes *P. coromandelica*. *Metapenaeopsis barbata* occurs in offshore catches along with other species of this genus and other genera.

The present annual catch from the Udang prawn fisheries is of the order of 25.0×10^3 tons altogether, this figure being dominated by the west coast and Malacca Strait total of 21.0×10^3 tons. There are no exact data on the status of these prawn stocks, but there may be some over-fishing in the inshore areas, while there are also considerable areas of mangrove and offshore grounds which are scarcely exploited. Thus, the fishery can withstand considerable increase in intensity, and a total of, say, 35.0×10^3 tons does not appear impossible for this fishery in the foreseeable future.

The fishery for Udang baring shrimps depends on several species of Acetes. In the south *Acetes vulgaris* comprises most of the catches, but in the north *A. sibogae* is important, while *A. erythraeus*, *A. spiniger*, and *A. japonicus* occur generally. Perhaps all species of this genus except the planktonic *A. serrulatus* are of some importance locally or seasonally. The catch may sometimes contain small quantities of mysids such as *Mesopodopsis* but these are seldom important. Production figures are approximately 5.7×10^3 tons for the west coast and Malacca Straits and there are no indications that the fishery is over-exploited, as these small prawns occur everywhere in immense numbers. It seems certain that the production figures could be raised to about 7.5×10^3 tons annually. The freshwater shrimp *Macrobrachium rosenbergii* is caught in estuaries, and is a valuable item of pond fish culture.

In addition to the above a fair quantity of small prawns is included in the landing statistics under the "mixed fish" and "manure fish" categories but there are no accurate data on the proportions. A fair percentage of beach catches certainly go unrecorded where they are used for local consumption by villagers, and there are also unrecorded subsistence fisheries in freshwater for *Atya spinipes*, species of *Macrobrachium* including *lanchesteri*, *geron*, *trompi*, *sintangense*, and *javanicum*. In our view all of these fisheries are currently neglibible.

Collections made by the former Singapore Regional Fisheries Research Station now held in the University of Singapore Zoology Department indicate that there may be commercial quantities of the pandalid prawn *Plesionika martia* along the upper part of the continental slope off northern Sumatra and north-western Malaysia, and this is entirely in agreement with assumptions that might have been made on the grounds of explorations in other parts of the tropical seas.

Finally, in the extreme south-eastern part of the region a trawl fishery is developing rapidly along the continental shelf of Western Australia, being presently concentrated mainly in Shark Bay and in Exmouth Gulf. Based on the exploitation of *Penaeus esculentus* (50% of production), *P. latisulcatus* (49%) and *P. merguiensis* (1%), this fishery has produced in recent years as follows:

1962—0.3	1966—1.2
1963—0.7	1967—2.2
1964—1.1	1968—1.4
1965—1.1	1969—2.1

Fishing operations reached Shark Bay in 1962 and Exmouth Gulf in 1964 and are presently extending to the northward; until this extension is completed, catches from this fishery will probably be regulated at somewhere near the present level by management procedures. A small fishery with handnets for *Metapenaeus bennettae* in the estuaries of Western Australia is not identifiable in currently available statistics and the landings are considered negligible for present purposes.

D. *Present production and future potential of Region VIII*

Apart from the coastline of north-western Australia the coasts of the Eastern Indian Ocean receive an abundant rainfall and the dominant species are those which spend a part of their juvenile lives in a fresh or brackish environment, and include: *Penaeus indicus*; *Metapenaeus monoceros*, *M. ensis*, *M. affinis* and *M. brevicornis*; *Penaeus semisulcatus* and *P. monodon* (which are appreciated for their size). Further offshore, species of *Parapenaeopsis* may dominate in the catches and note must be taken especially of the small *Macrobrachium rosenbergii* which extends from India to North Australia and is the most appreciated of the non-penaeid species. No studies have been undertaken on the status of any of the stocks in the Eastern Indian Ocean but there can be no doubt that throughout much of the region there appears to be little or no offshore exploitation which suggests that the resources in general are under-exploited. The Table indicates the present production of the various types of resource from each country in the region together with a tabulation of the estimates that have been made in the text on the potential resources. It is to be noted that the figure of 53.0 as the potential production from the Eastern Indian Ocean excluding Malaysia and Western Australia is derived from the estimates of Hall, who based his figures on an area, and catch rate per area basis.

	Present	Potential
	(tons × 10³)	
Spiny lobsters		
Western Australia	8.6	8.0
Crabs		
Region	+	+
Prawns and shrimps		
Ceylon, east	1.5	53.0
India, east	10.5	
Pakistan, east	7.8	
Burma	5.0	
Thailand	4.8	
Indonesia	0.8	
Malaysia	26.7	42.6
Australia	2.1	5.0
Total	67.5	108.6

Region IX—Western Central Pacific

This includes most of Oceania, the coast of Asia from Japan to Singapore and the islands and archipelagos lying between Japan and New Guinea. Much of the region consists of enormous reaches of open ocean, sparsely studded with small islands, but paradoxically it also includes the greatest area of continental shelf occurring within tropical latitudes. The archipelagos of the Philippines and Indonesia, together with the smaller island clusters and the coast of southeat Asia, include an immense length of tropical coast line (there being 14.0×10^3 islands in the Philippines alone). This is a region of heavy rainfall and many rivers, creeks and lagoons open onto the continental shelf, and the coast itself is often low-lying and includes many sheltered, low salinity, muddy bays and gulfs. It is no surprise, therefore, to find that the statistics indicate a wealth of prawn resources, perhaps the greatest in the tropical seas, and largely unexploited.

A. *Spiny lobsters and similar resources*

The fishery for spiny lobsters is small by comparison with that of Australia and New Zealand, but some are taken in many places, notably Japan (1.6×10^3 tons per year), and Taiwan (0.1×10^3 tons per year). It is probable that in many places the landings of spiny lobsters are hidden in statistics of other crustaceans, rather than being identified specifically.

Spiny lobsters occur throughout the tropical regions and are probably an extremely under-exploited resource in this region; although population densities are unlikely to be high in tropical latitudes the stocks are sufficient to support small fisheries. A few vessels from New Zealand have, at times, fished the Kermadecs and Tonga, among other islands.

It seems probable that an estimate of 5.0×10^3 tons is not too high an estimate for the potential annual yield from the whole of this vast region. Similar species, such as the *Nephrops andamanica* which occurs along the continental edge off Hong Kong, would contribute to this total. Flapjack lobsters, *Thenus orientalis*, are caught in the Gulf of Thailand and on a small scale off Malaysia and Singapore, but there are no exact figures on production.

B. *Crab resources*

Many species of crabs are taken throughout the region; though not specified in most of the statistics, these appear to be largely portunid swimming crabs of several genera with *Scylla servata* and *Portunus pelagicus* predominating. This fishery is homologue of the blue crab fishery in the Western Atlantic.

Known catches of crabs in the region in 1965 were:

	(tons × 10³)
Malaysia	1.5
Thailand	11.0
China (Taiwan)	1.8
Japan	25.0
Total	39.3

It may be safely assumed that the real catches of the region are actually at least 50.0×10^3 tons per year, since in many places (such as the Philippines) crabs are certainly caught, but are not identified in the available statistics.

The relatively short coastline of the eastern seaboard of the USA produces about 75.0×10^3 tons of *Callinectes* per year at close to maximum exploitation levels; it is not unreasonable to suppose that Region IX, with its very much greater shelf area and length of coastline could produce twice this quantity or 150.0×10^3 tons per year. This may be a gross under-estimate and the appropriate factor may rather be ×10 than ×2.

C. *Prawn resources*

Here the data are rather better, and it will be convenient to discuss the resources by five sub-regions.

(i) The Sunda Islands and New Guinea

Indonesia

Data are rather sparse, but suggest that the resources are large and under-exploited. No detailed statistical data exist on present fisheries, which Ivanov (1964) places at 2.5×10^3 tons, and which primarily exploit *Penaeus indicus* and *Metapenaeus ensis*, though it is reasonably certain that all species which are of economic value in Malaysia are also fished by Indonesia. It is known also that Belachan shrimp (*Acetes* sp.) are exploited, as are Terasi (juvenile penaeids, etc., and Mysidacea) for use as shrimp paste. Freshwater *Atya* and *Caridina* are also fished on a subsistence scale in many areas, especially in the Celebes.

In general, this area is very rich in prawn resources, and Malaysian fishermen consider it to be richer than their own waters; although the results of Indonesian resource surveys off Java and West Irian are yet to be published, it is reasonable to suppose that a potential of 100.0×10^3 tons is not too high for Indonesia. This, is, however, purely conjectural.

Brunei

Contiguous to grounds exploited by Malaysian fishermen, there is known to be a small fishery here which primarily exploits *Penaeus merguiensis.* No production data are available, but it is probably less than 1.0×10^3 tons.

Sabah

Some 21 species of penaeids are known to occur in the local fishery, and *Penaeus indicus* and *P. merguiensis* are the most important; the present production is about 3.0×10^3 tons per year, heads-on, from an estimated exploited area of 7.0 to 10.0×10^3 km^2.

Control measures exist and only the western fishery region seems likely to be capable of expansion, to an uncertain extent. It is suggested that a fishery for *Acetes* spp. could be developed in mangrove areas, as in Brunei and Malaya.

A total potential of 4.0×10^3 tons may be reasonably deducted from these observations.

Sarawak

Fishing is still on a small scale and though prawns (mostly *Penaeus indicus, P. monodon, P. merguiensis* and four species of *Metapeneaus*) are known to be present in commercial quantities, no production figures or estimates of potential are presently available. It is assumed here that a catch of at least 1.0×10^3 tons is possible annually.

Timor and Papua/New Guinea

No data are available for this area, though it is evident that resources must exist. From the size of the area, it seems that at least 10.0×10^3 tons could be taken.

Northern Territories, Australia

Exploitation of the northern, tropical prawn resources has only just begun, following resource surveys by CSIRO which indicate that the potential of this region exceeds that of the rest of Australia several-fold. A prawn-fishing base has been established on the Gulf of Carpentaria at Karumba, where 14 vessels landed 0.45×10^3 tons in 1967, and 40 vessels 1.36×10^3 tons up to August in 1968. Catches by mother-ship fleets of Japanese trawlers in the Gulf are not known, but are probably similar to the above.

The CSIRO resource surveys in the tropical northern regions indicate a potential of 11.4×10^3 tons for the Gulf of Carpentaria or 20.0×10^3 for the whole of the northern territory, and these estimates are certainly conservative.

(ii) Oceania

Tahiti

The only data available suggest a very small fishery for *Macrobrachium lar*, at subsistence level, and with a production probably $< 1.0 \times 10^3$ tons.

Tonga

Some prawns are taken on a subsistence basis.

Samoa

Prawn resources are known to occur, but identity and magnitude entirely unknown.

Fiji

A resource survey indicates the presence of stocks of *Penaeus monodon* in commercial concentration, but no fishery has developed and potential is not known. A subsistence freshwater fishery for *Macrobrachium lar, M. australe* and *M. latimanus* occurs, but there are no production data although fishing is said to be "quite heavy", and extension seems likely.

Guam and Marianas

There is a small subsistence fishery for *Macrobrachium lar*. Potential is very limited.

(iii) Asian coastline

Singapore

Prawn trawling offshore is incidental to fish trawling and only the larger prawns are saved from the catch; these include the following species: *Penaeus indicus, P. monodon, P. semisulcatus, Metapenaeus intermedius, Parapenaeopsis probata, P. hardwickii, Metapenaeopsis barbata,* and *M. merguiensis.* About 0.4×10^3 tons are obtained this way each year, and although there is no indication of the extent of potential fishing grounds, it is believed that offshore stocks would sustain a specialized fishery for prawns. It is rather likely that the potential for the offshore South China Sea coast of Malaya and Singapore would be at least 10.0×10^3 tons annually.

A varied catch is made of other, inshore, species of prawns with a variety of gear, mostly on a subsistence level, based on: *Metapenaeus affinis, M. lysianassa, Parapenaeopsis* spp., *Metapenaeopsis* spp., *Acetes* and *Palaemon.* Some of these catches are made incidentally in beach fishing. Production from such means approximates 0.4×10^3 tons at present.

Pond culture of penaeids produces 0.1×10^3 tons per year, 97% of the production comprises *Penaeus indicus, Metapenaeus burkenroadi, M. brevicornis.* Also important are *Penaeus monodon* and *P. semisulcatus* because of their high individual value.

Malaya (Johore and East Coast)

There is a fishery here which depends on the same species as at Singapore, and in which *Penaeus indicus, Metapenaeus ensis, M. burkenroadi* and *M. affinis* are dominant. Total production from this area is currently 3.4×10^3 tons, and there are indications that some of the inshore areas are already over-fished, though great areas of mangrove remain to be exploited; offshore areas are relatively virgin, but their potential is included in the offshore area discussed for Singapore. A potential, excluding offshore reaches of the South China Sea, of 5.0×10^3 tons seems probable for this area.

Thailand

Prawn catches by the Thai fishery in the Gulf and South China Sea adjacent have increased significantly in recent years:

(tons × 10³)	
1958—10.3	1965—35.2
1959—23.3	1966—45.3

Commercial samples and non-official data suggest that prawns are the mainstay of the Gulf of Thailand fishery, which is based on *Penaeus merguiensis*, *P. indicus*, *P. monodon*, and *P. semisulcatus*, together with some *Metapenaeus* spp. and *Metapenaeopsis barbata*, *Parapenaeopsis* spp. and finally *Acetes* spp. inshore.

From the manner in which the catches have been rising in recent years and from surveys such as those by Tiews (1965) it seems likely that although some increase is possible this may well not result in a rise beyond 50.0 × 10^3 tons, which will be used here as the potential of the fishery.

A small fishery for the freshwater *Macrobrachium rosenbergii* and *M. lanchesteri*, and brackish to freshwater species of *Alpheus*, produces about 5.0 × 10^3 tons annually; nothing is known the state of this fishery or of its potential for expansion.

Khmer Republic

A total of 0.5 × 10^3 tons of miscellaneous crustacea are taken annually, but it is not known what part of this total is formed by prawns; *Penaeus monodon* is known to occur in this catch, however. Status and potential of this fishery is unknown.

Vietnam

Published statistics suggest that catches in southern Vietnam before the present crisis amounted to 29.0 × 10^3 tons annually and catches in the northern part of the country may have been on the same order of magnitude. There appears to be no information as to the composition of the catch but at least in the south it is probably similar to the Thai catch. For present purposes, a potential catch of 50.0 × 10^3 tons is assumed for the whole of Vietnam since there are no data on which to estimate the potential of the resource more objectively.

China (mainland)

"Though no exact figures are available, the Chinese People's Republic is undoubtedly one of the largest shrimp producers in the world" (Ivanov 1964).

Ivanov further suggests that 100.0 × 10^3 tons of prawns are taken annually, of which 70.0 to 80.0 × 10^3 are from the Yellow Sea and are dominated by *Penaeus orientalis* and *Acetes chinensis*. Although the East and South China Sea have a more varied fauna of prawns and shrimps, the Yellow Sea is much more productive commercially.

Most of the production is by small boats at present and probably 90% of all products are consumed by the coastal population, though some is exported to Japan.

For the present purposes, the figure of 100.0 × 10^3 tons perhaps should be retained as the potential of the resource, but an increase by a factor of 1.5 seems very likely with eventual resource management and offshore exploitation, and 150.0 × 10^3 is taken as the potential of the area.

Hong Kong and Macao

Nineteen species of penaeid prawn occur in the Hong Kong catches, and presumably those at Macao are rather similar in composition. The catches seem to be dominated by *Penaeus semisulcatus*, *P. monodon*, *P. merguiensis*, *Metapenaeus intermedius* and *M. affinis*.

Latest production figures available for Hong Kong and Macao are for 1965 when 10.4 and 4.0 × 10^3 tons respectively were taken from around 8.0 × 10^3 km² of fishing grounds. Although nothing certain is known, it is believed that the catches can be increased, and the potential is thought to be in the region of 20.0 × 10^3 tons.

(iv) The Asian Islands

Philippines

The marine catches are now about 20.0 × 10^3 tons annually, including *Penaeus indicus*, *P. merguiensis*, *P. monodon*, *P. semisulcatus* (= *P. canaliculatus*?), *P. esculentus*, *Metapenaeus ensis*, *M. burkenroadi* and *Trachypenaeus curvirostris*. Although research is presently being conducted in the Philippines on the rather undeveloped prawn trawl fishery, little information is presently available from it; a catch of at least double the present production would seem attainable, and 50.0 × 10^3 tons is taken as the potential of this sub-region.

As usual in this region, small quantities (production figures lacking) of *Macrobrachium lar* and related species are taken in freshwater.

Taiwan

A prawn trawl fishery exists in which *Penaeus monodon* appears to figure rather largely, and for which there are few data beyond the total production which is presently around 14.5 × 10^3 tons (the 1965 figure). Since Taiwan has a much shorter coastline and smaller shelf area than the Philippines there appears to be no justification for supposing that a very great increase in landings might be possible, and the potential increase used here is a very modest 10%, to give a total of 16.0 × 10^3 tons. It should be noted that the shallow, wide shelf areas of Taiwan face westwards towards the Chinese mainland, and any potential here will be shared between the two fisheries.

Japan

The Japanese are major producers of shrimps and prawns, their 1965 catch being in the region of 66.6 × 10^3 tons; a portion of this came from the Northern Pacific (Bering Sea and Gulf of Alaska) and a portion from the Guianas and Australia, outside Region IX. The prawn catch from the Western Central Pacific has declined in recent years; after 1963 it is not possible to separate it in available statistical data from total landings:

(tons × 10^3)
1961—53.7 × 1.5 = 80.5
1962—52.9 × 1.5 = 79.3
1963—51.0 × 1.5 = 76.5

(production statistics are as "heads-off" weights, and a factor is applied above, and throughout this section).

If the known Bering Sea catches are subtracted from the 1965 total it appears that the Western Pacific total by 1965 may have dropped to as low as 55.6 × 10^3 tons, heads-on, but may have been higher than this, there apparently being some confusion in the data.

The bulk of the landings from the Western Central Pacific region are taken in (1) the Inland Sea, and (2) the Yellow Sea.

In the Inland Sea and similar home-island fishing areas *Penaeus japonicus* forms 25–35% of the catches, but about twice that percentage of their value. *Metapenaeus joyneri* forms about 20%, the small species *Trachypenaeus curvirostris*, *Metapenaeopsis barbata* and *Parapenaeopsis tenella* about 45%, and the large, valuable species *Penaeus monodon* and *P. semisulcatus* about 5%.

The fisheries in the Yellow Sea, the East China Sea and the Korean Bight, which produced about 1.0 × 10^3 tons annually in the early 1960s, are dominated by the oceanic *Penaeus orientalis*, which occurs in rather deep water, where it is fished by larger shrimp trawlers, especially between November and March.

There are no suggestions in the data now available for review that a potential for increase exists in the Japanese warm-water prawn fishery except in the distant waters of other areas of the Western Central Pacific region. It is likely that any expansion which might be possible in the offshore resources, such as in the *Penaeus orientalis* fishery, might be offset by losses in the nearshore fisheries, especially those of the Inland Sea, due to industrial and agricultural pollution and competition from other uses of these sea areas. A total of 60.0 × 10^3 tons, heads-on, annually is therefore used here as the long-term production to be expected from this area.

(v) Pond production

Pond production of larger species of marine prawns is practiced in several places within the region, and fractionally increase the total prawn production of the region. Recent data on prawns from these sources follow:

		(tons × 10^3)
Philippines	*Penaeus monodon*	1.0?
Singapore	15 spp. Penaeidae	0.1
Japan*	Various *Penaeus* spp.	0.3
Indonesia	Madura, Java	6.2
	Coastal ponds	3.0
China (Taiwan)	*Penaeus monodon*	?
		<10.0

* Ivanov, 1964, gives 2.0 × 10^3

The data and available information on this form of production show several things rather clearly: that while in some places there are great possibilities for extending pond area and production, in others it is a diminishing resource because of urban and other encroachment (e.g. Singapore); that production is either of high value, preferred species (as in Japan) in which case production sites must be near centres of demand, or of many small species of penaeids, caridians and mysids which are used for biological reduction to paste or for drying; and that production is highest where local populations have a tradition of animal husbandry and pond culture of various fishes, without which its introduction into a new area is probably difficult.

With these limitations, evidently it is not possible to place a limit on the possible expansion of pond cultured prawn production: geographic and economic factors, presently impossible to assess, are limiting and it is now only possible to point to the relatively small proportion this production forms of the total for the region and to indicate that it seems unlikely ever to form more than 10–25% of present production.

Ivanov (1964) and Iversen (1968) give good reviews of prawn culture in this region.

D. *Total crustacean potential*

The above discussion of the regional production at the present time has been reviewed below; this indicates a total crustacean production of 323.1 × 10^3 tons whole weight annually. This does not correspond with the FAO annual statistics of fisheries because it is compiled from numerous sources, not all referring to the same year; it simply confirms that the total production of crustacea, over and above subsistence level catches which do not enter statistical data bases in most areas, is probably near 350.0 × 10^3 tons annually in this region in recent years.

Using the various projections, which are necessarily of different validity and usefulness, that are used in the preceding discussions, a total production or around half a million tons of crustacea annually seems possible for this region: this may only be an order of magnitude projection, but serves at least to emphasize the great potential of the area. To this figure must be added about 10.0 × 10^3 tons for freshwater production and perhaps 50.0 × 10^3 tons for pond production, giving a grand total of 604.1 × 10^3 tons.

	Present	(tons × 10^3)	*Potential*	
Spiny lobsters				
Japan	1.6		5.0	
Taiwan	0.1			
Oceania	+			
		(1.7)		(5.0)
Crabs				
Malaysia	1.5		150.0	
Thailand	11.0			
Taiwan	1.8			
Japan	≈25.0			
		(39.3)		(50.0)
Prawns				
(Sea)				
Indonesia	2.5		100.0	
Brunei	<1.0		1.0	
Sabah	≈3.0		4.0	
Sarawak	?		>1.0	
Timor/New Guinea	?		>10.0	
Australia, Northern Territories	3.0		>20.0	
Tahiti	?		>1.0	
Tonga, Samoa, Fiji, Guam	+		+	
Singapore	0.8		10.0	
Malaya	3.4		5.0	
Thailand	35.2		50.0	
Khmer	0.5		0.5	
Vietnam	50.0		50.0	
China (Mainland)	100.0		150.0	
Hong Kong/Macao	14.3		20.0	
Philippines	20.3		50.0	
China (Taiwan)	14.5		16.0	
Japan	55.6		55.6	
Total		(304.1)		(544.1)
Prawns				
(Freshwater)	10.0		10.0(?)	
(Ponds)	<10.0		50.0(?)	
Grand Total	323.1		604.1	

Region X—Eastern Central Pacific

For the purposes of this review, Region X has been taken to include the western seaboard of the American continent from the northern boundary of California (42°N) to the boundary Ecuador/Peru.

A. *Spiny lobster resources*

Spiny lobsters of a number of species occur the whole length of the region, but catch statistics are available only for Ecuador (0.3 × 10^3 tons in 1965) and Mexico (1.2 × 10^3), and in the latter case the data refer to both east and west coast catches combined.

In Mexico, a fishery occurs along the Pacific coast of Baja California for *Panulirus interruptus* and *P. inflatus*, and along much of the coast of the Gulf of California and of Sonora and other west coast states for *P. inflatus*; much of this production finds it way to US markets, but statistics on it are meager. It seems certain that increased production is possible, but could not be expected to exceed 5.0 × 10^3 tons annually for the whole of Region X, and this figure, probably too large, will be used as an order-of-magnitude estimate for present purposes.

B. *Crab resources*

Crabs do not appear in any of the available fishery statistics for the region except in the case of Mexico, and here the catch figures, totalling 1.5 × 10^3 tons in 1965 again include both east and west coasts of the country. It is certain, that as in most tropical regions, the crab resources are under-utilized; many species of portunid swimming crabs occur, some of large size, and (once again) reference should be made to the Callinectes production of the eastern seaboard of the USA, in comparison with the very small landings in Region X. It is probable that an increase in production by a factor of at least 10 would be possible, but a more modest estimate based on a factor of only 5 is used here, to suggest that the crab potential of the region may be placed for present purposes at 7.5 × 10^3 tons annually.

C. *Prawn resources*

About 10 species of penaeids figure in the landing statistics in Region X, and these are listed below. The species composition in the landings is rather constant throughout the region, which is faunistically fairly uniform, having important faunal boundaries to the north and south. Information for Mexico and for Ecuador is not so detailed as for the remaining six countries, but there is no reason to suppose that much of the information relevant to these countries is not also relevant to Mexico and Ecuador. Ivanov (1964) indicates that even in the ecologically unique Gulf of California the important species are among those listed below as being important further to the south.

(a) White shrimp—Camaroncillo	*Penaeus vannamei* *P. occidentalis* *P. stylirostris*
(b) Brown or white—Café o blanco	*P. californiensis*
(c) Pink or red—Rojo	*P. brevirostris*
(d) Seabobs, tiger—Camaroncillo	*Trachypenaeus byrdi* *T. similis* *T. faoea*
(e) Seabobs—Titi	*Protrachypene precipua* *Xiphopenaeus riveti*

Although some mixing among stocks of prawns probably occurs between neighbouring countries, especially in Central America, all fishing fleets operate off their own national coasts and the fishing effort in relation to the available resources varies markedly; for these reasons, the data for landings and fishing effort for each country are here kept separate.

Relative abundance of species in the landings may not have any ecological significance: because *P. californiensis* and *P. brevirostris* live relatively deep, they are normally fished for only when shallower-living species are scarce, and the relative abundance of the various species of seabobs in the landings do not necessarily indicate their relative abundance on the grounds. In most fisheries, seabobs are frequently discarded at sea when prices are not favourable.

Fishing effort is primarily directed at white shrimp (*P. occidentalis*, *P. stylirostris*, *P. vannamei*, plus, in Panama and Costa Rica, *P. californiensis*). Adults of these species have similar ecologies and it is likely that their relative abundance in the landings does, in fact, represent their real abundance on the grounds. Some variation in relative abundance occurs: in Colombia, *Penaeus occidentalis* forms the bulk of the landings, as in Ecuador and Panama, but farther north, in El Salvador, it forms only about 30%. Here and northwards *P. vannamei* attains dominance in the landings.

The shrimp resources show marked local concentrations throughout the region off the mouths of rivers and estuaries, and in muddy bays and gulfs; small fisheries occur in the brackish areas of estuaries, lagoons and embayments but there are no statistical data on these, which seem to be directed at the juvenile stages of several important species of white shrimp, especially *P. vannamei* and *P. stylirostris*.

Landing data for white shrimp are more detailed than for the other groups and in most countries include effort and size frequency information.

In each country, the landings of white shrimp increased as the fleet built up while the catch per unit effort declined from an initial high. As this process developed, trips were made into progressively deeper water and fish and brown shrimp began to appear in the landings and the larger seabobs, previously discarded, began to be landed. In most countries the fishery for white shrimp appears to be stabilized, though there are considerable yearly fluctuations in availability; with the possible exception of Nicaragua, it seems that little increase in yield is possible except by curtailment of effort.

The landings of seabobs have fluctuated independently of the fishing effort and economic and technological factors have been casual. A further modest increase in seabob landings is clearly possible when it becomes economically practicable, especially for *Protrachypene* and *Xiphopenaeus*.

The landings of red and brown shrimp appear to be relatively stable but their exploitation is probably limited by the limited capabilities of the trawlers in the present fleets for trawling in deeper water, below about 50 fm, and perhaps by a coincidence of the time of their peak abundance with that of white shrimp, always the preferred object of the fishery.

TOTAL LANDINGS, ALL PRAWNS (TONS × 10^3)

	1961	*1962*	*1963*	*1964*	*1965*	*1966*	*1967*
Ecuador	6.4	6.7	5.2	5.0	5.7	+	+
Colombia	1.8	1.8	0.9	1.0	0.9	1.0	+
Panama	5.5	6.1	5.6	7.1	5.9	5.6	+
Costa Rica	0.9	1.0	1.0	1.2	1.1	1.1	1.2
Nicaragua	+	+	+	+	0.3	0.9	0.9
El Salvador	3.9	3.8	3.5	8.5	3.1	4.6	3.5
Guatemala	0.6	1.0	0.8	1.3	0.8	1.4	1.1
Mexico	54.2	52.0	52.9	51.7	44.3	41.7	42.9
Total	(73.3)	(73.3)	(69.9)	(70.8)	(62.1)	(61.0)	+

It appears from the data presently available that the total prawn production in the region is about 65.0 × 10^3 tons; it is not unreasonable to suppose that increased effort on fish and brown shrimp, and decreased discarding of seabobs could certainly raise the annual production to at least 75.0 × 10^3 tons per year, which is taken as a conservative estimate for present purposes.

D. *Galatheid resources*

Five species of galatheid crabs are known to exist in mass occurrences, mostly in highly eutrophic regions of the ocean. Two of the species (*Munida gregaria* and *Pleuroncodes planipes*) occur in vast pelagic swarms as juveniles or young adults, and both species graze on diatom blooms when in the pelagic phase. These two species, and *Munida subrugosa* of the sub-Antarctic and *Cervimunida johni* and *Pleuroncodes monodon* of Chile also occur in massive benthic concentrations, usually of larger individuals.

Off both coasts of Baja California, *Pleuroncodes planipes* occurs in vast concentrations in both the pelagic and the benthic phase. It has also been found between Costa Rica and Mexico in 150–250 m. It appears likely that a fishery could be developed for it, and catch rates of 2.5 tons per hour with a 30 m^2 mid-water trawl are likely. The fishery for galatheids off Chile and Peru has been suggested to have a potential production of 50.0 × 10^3 tons per year, and it seems certain that at least half this quantity could be taken from the bottom-living stocks of *Pleuroncodes planipes* on a sustained basis. A potential of 25.0 × 10^3 tons per year is, therefore, used for our present purposes. (A suggestion that potential could be extremely large, taking into account the pelagic phase of *Pleuroncodes* is given in the section on oceanic resources.)

E. *Total regional potential yield*

This may be derived from the following tabulation which groups the estimates discussed above:

	Present (tons + 10^3)	*Potential*
Spiny lobsters	?	5.0
Crabs	<1.5	7.5
Prawns	65.0	75.0
Galatheids	—	25.0
Total	66.5	112.5

LANDINGS AND LANDINGS PER UNIT EFFORT FOR FOUR GROUPS OF PRAWN SPECIES

Species	*Landings—tons × 10^3 per year*							*Landings(kg) per boat per day*						
	61	*62*	*63*	*64*	*65*	*66*	*67*	*61*	*62*	*63*	*64*	*65*	*66*	*67*
Guatemala														
White shrimp			0.2	0.3	0.3	0.4	0.2			40	60	48	52	29
Brown shrimp			0.5	0.5	0.4	0.5	0.4			130	161	121	114	50
Pink shrimp			+	×	0.05	0.1	0.2			+	+	5	21	23
Seabobs			0.2	0.5	0.2	0.4	0.2			46	85	36	59	26
El Salvador														
White shrimp	1.8	1.6	1.6	1.7	1.0	1.6	1.0	115	98	92	90	56	80	54
Brown shrimp	0.5	0.1	0.1	0.1	0.04	0.1	0.1	114	104	97	96	60	85	58
Pink shrimp	0.8	0.5	0.5	0.4	0.5	0.5	0.4	49	34	26	20	23	25	21
Seabobs	0.9	1.5	1.3	1.2	1.6	2.4	2.0	61	93	71	64	84	122	101
Nicaragua														
White shrimp					0.1	0.5	0.3					82	137	74
Brown shrimp					0.1	×	0.05					115	166	85
Pink shrimp					0.1	0.3	0.3					55	93	67
Seabobs					×	0.1	0.2					×	53	48
Costa Rica														
White shrimp	0.4	0.3	0.3	0.5	0.3	0.3	0.3	×	31	31	63	29	31	×
Brown shrimp		×	×	×	×	×	×	49	×	×	×	×	×	×
Pink shrimp	0.1	0.2	0.2	0.1	0.1	0.1	0.2	9	23	17	9	16	14	×
Seabobs	0.5	0.5	0.6	0.6	0.6	0.6	0.5	71	62	63	68	78	57	×
Colombia														
White shrimp	1.0	1.0	0.8	1.0	0.9	1.0		86	74	85	113	102	106	
Brown shrimp	+	+	+	+	+	+			+	+	+	+	+	
Pink shrimp	+	+	+	+	+	+		+	+	+	+	+	+	
Seabobs	+	+	0.2	+	+			×	×	20	+	+	+	
Panama														
White shrimp	2.1	2.0	1.6	2.3	2.3	2.4	+	×	56	39	41	38	43	
Brown shrimp		+	+	+	+	+	+	59	+	+	+	+	+	
Pink shrimp	1.2	1.5	1.3	1.1	1.3	1.2	+	33	42	33	21	22	21	
Seabobs	2.2	2.4	2.7	3.6	2.3	2.1	+	62	66	67	67	38	38	

Region XI—Southwest Atlantic

This region has a very great latitudinal extent from the eastern border of Venezuela down to the southern tip of South America continent and the Falkland Islands; this encompasses a very considerable diversity of ecosystems from tropical continental shelves in the north, much influenced by the great rivers of Surinam and Brazil, through the sub-tropical continental shelves of southern Brazil and Argentina, to the Antiboreal regions of the south. As might be supposed, the major crustacean resources are those for shrimp in the regions of the major tropical river mouths, particularly in northern Brazil, Surinam and the Guianas, and also in the region of the rather extensive coastal lagoons and estuaries between northern Argentina and southern Brazil.

A. *Lobster resources*

There is a valuable fishery for spiny lobster, mainly *Panulirus argus* and *P. laevicanda*, along the coast of central Brazil from Belem to Santos; peak catches in recent years were made in 1962 when 4.3×10^3 tons were taken (Boschi), although the FAO statistics show a rather smaller number (2.9×10^3 tons) for this year. This stock has been the object of international fisheries in some years, having been exploited not only by local boats, but also by French langoustiers fishing for the French domestic market. It is probable that this stock is fairly heavily fished and no great increase in sustainable yield can be expected from it. For present purposes its potential is considered to be 4.0×10^3 tons, or near the present production. Negligible quantities of this species, and of other spiny lobsters, are taken off the coast of Surinam and the Guianas.

B. *Crab resources*

Rather more than 15.0×10^3 tons of crabs of various species, mostly swimming crabs of the family Portunidae, are taken on the Brazilian coast south of Santos. There are no data on the degree of exploitation of these resources or on their future potential which is here taken to be 20.0×10^3 tons, to reflect the steady increase in production in recent years.

C. *Shrimp and prawn resources*

The shrimp and prawn resources of this coast which are presently exploited comprise approximately 12 species which are tabulated below. The FAO landing statistics for shrimps and prawns for the east coast of South America indicate clearly that Brazil is the dominant producer followed rather distantly by Guiana.

Guiana

Until 1959, the only production of shrimps in Guiana were from the inshore Chinese shrimp nets which took only small quantities of the very small *Palaemon schmitti* and *Hippolysmata oplophoroides*. However, in 1959, offshore explorations by US shrimp boats discovered good stocks on the continental shelf of very large penaeids, and the recently increasing production year-by-year is due to initiation of production from these sources. The offshore stocks appear to be dominated by *Penaeus duorarum notialis* and by *Penaeus aztecus subtilis*. The former comprises about 80% of the landings from these stocks, and the latter only about 20%. Production is now probably in excess of 5.0×10^3 tons, and potential is expected to be at least 10.0×10^3 tons annually.

Surinam

In this country the situation is rather similar to that in Guyana, and until recent years only inshore stocks of seabobs (*Xiphopenaeus kroyeri*) were exploited, but more recently continental shelf stocks of penaeid shrimps, which appear to be dominated by *Penaeus brasiliensis*, have been discovered offshore at around 50 m depth and these have increasingly contributed to the landings as a small fleet of shrimp trawlers has built up. The catches from the continental shelf from Guyana, Surinam and the neighbouring territory of French Guiana have now reached together approximately 6.0 to 7.0×10^3 tons annually, and further increases can be looked for. It is quite certain that this production figure can be at least doubled, and a total potential of at least 15.0×10^3 tons is postulated here.

Brazil, north of Recife

This includes the rich area of the mouths of the Amazon and other rivers where the continental shelf is wide and all exploratory evidence points to there being extremely rich under-exploited stocks of penaeids. Present production from this region is 10.0 to 15.0×10^3 tons annually and is dominated by the small seabob *Xiphopenaeus kroyeri*, which forms about 60% of the production from this area, and there are indications that very large stocks

DISTRIBUTION OF KNOWN SHRIMP RESOURCES, REGION XI; ++ = IMPORTANT STOCKS, + = LESS IMPORTANT STOCKS; A–RIVERINE, B AND C—INSHORE, D—CONTINENTAL SHELF, LOW LATITUDES, E—CONTINENTAL SHELF, HIGH LATITUDES

		Guiana	*Surinam*	*N. Brazil*	*S. Brazil*	*Uruguay*	*Argentina*
A	*Macrobranchium amazonicum*	+	+	+			
	M. carcinus, et al.	+	+	+			
B	*Palaemon schmitti*	+	+	+			
	Hippolysmata oplophoroides	+		+			
C	*Xiphopenaeus kroyeri*	++	++	++	+		
D	*Penaeus schmitti*	++	+	+	+		
	P. aztecus subtilis	++	+	++	+		
	P. brasiliensis		+		+		
	P. duorarum notialis	++		++	+		
	P. paulensis				++	++	
E	*Hymenopenaeus muelleri*				+	+	++
	Artemesia longinaris				+	+	++

of larger, commercially interesting penaeids (including *Penaeus schmitti* and *P. aztecus*) occur along most of this coastline although they are of course especially concentrated near the mouths of the great rivers. Potential is expected to be relatively high and 25.0×10^3 tons seems a conservative estimate.

Brazil, south of Recife

There are two main centres of production of prawns in this area, both of which are probably determined largely by the occurrence of centres of human population rather than for other reasons. In the extreme south from the Doce River to Lagoa do Patos there are active shrimp fisheries off the mouth of the Rio Grande and while in the vicinity of São Paulo shrimp fisheries are again rather active. A number of species of penaeids are taken and these appear to be dominated rather heavily by *Penaeus brasiliensis*, which certainly dominates the Rio Grande fishery; from January to May the young of this species migrate out of the rivers and estuaries at the peak fishing season. Year-to-year fluctuations are very considerable and appear to be very largely under climatic influence, for in wet years the lagoons are too fresh for the production of large numbers of juveniles and a poor fishery results. The production over the last few years from the Rio Grande fishery is as follows:

(tons × 10^3)	
1956—17.3	1960—23.4
1957—20.6	1961—26.1
1958—18.5	1962—35.2
1959—19.5	1964—27.2

Potential production from this area is postulated here to be equal the highest annual production quoted above; with a modest allowance for the rest of the coast a total of 40.0×10^3 is postulated. Freshwater prawns (*Macrobrachium*) are, of course, important throughout the Amazon basin and production must be far greater than the 2.6×10^3 tons recorded statistically in 1967. It is not possible to guess logically a quantity for total potential production.

Uruguay

The present landings of shrimps and prawns, as of other crustacea from Uruguay, are negligible, though the occurrence of *Penaeus paulensis* in coastal lagoons in this country and of the northern part of the great estuary of the Rio de la Plata suggest that some potential for expanded production exists; if this occurs, it will in all probability also be based upon *Hymenopenaeus muelleri* and *Artemesia longinaris*. A potential of 1.0×10^3 tons is used here.

Argentina

There is very little information from the southern area of Argentina, and in the north shrimp catches, mostly of langostino (*Hymenopenaeus muelleri*) and camaron (*Artemesia longinaris*) have fluctuated in recent years very widely between 200 and 3,240 tons; these fluctuations are probably caused by fluctuations in spawning success and larval mortality rather than the effect of the fishery which presses rather lightly upon the resources. Surveys in the southern part of Argentina have indicated possibilities for expanded production; in the Patagonian area (particularly in the region of the Gulf of San José) some samples of large ripe females of *Hymenopenaeus muelleri* have been taken and offer the possibility of a fishery there for this species. There are also indications of the presence of deep water prawns and other crustacea of commercial interest off the coast of southern Argentina at depths around 100 m between 54 and 55°S, and a little further to the north the German research vessel *Walther Herwig* took commercially interesting quantities of a large species of sergestid shrimp, at depths of from 300–500 m with a mid-water trawl. This ship also took quantities of *Campylonotus*, *Nauticaris* and *Nephrops* in the waters between Buenos Aires Province and southern Brazil and Uruguay. Although these indications are slight and preliminary they do suggest that the occurrence of extensive deep water resources off the southern part of Argentina are at least a possibility. A potential of 5.0×10^3 tons is used here for all small natant crustacea. Between 44° and 55°S, *Lithodes antarticus* is fished off Patagonia and Tierra del Fuego, and catches total about 0.25×10^3 tons annually and a potential of 1.0×10^3 tons may be assumed.

D. *Potential production from Region XI*

The present and potential production from this region so far as it can be estimated from present data are indicated below:

	Present	*Potential*
	(tons × 10^3)	
Lobsters		
Brazil	3.5	4.0
Guianas	+	+
Crabs		
Brazil	15.0	20.0
Argentina	0.8	1.0
Prawns		
Guyana	>2.0	15.0
Surinam	>2.0	
French Guiana	>2.0	
Brazil	30.0–40.0	65.0
Uruguay	0.1	1.0
Argentina	1.0	5.0
Total	>56.4–66.4	111.0

This suggests that a doubling of present production may be possible and brings the total to about half the production from the Gulf of Mexico and Caribbean to the north; this suggests that the estimate may be too conservative, in consideration of the very great production to be expected off the mouth of the Amazon and the other rivers of northeast South America.

Region XII—Southeast Atlantic

The region extends from the northern border of Angola south through the region of the Benguela Current, and includes the coasts of the Republic of South Africa; to this extent it is an unnatural region as it extends around Cape Agulhas into the Indian Ocean, and includes part of the Indo-Pacific fauna along the coast of Natal.

A. *Spiny lobster resources*

A number of species of spiny lobster occur throughout this region and one of them (*Jasus lalandii*) forms the basis of an important fishery in southern Africa. The tropical west African *Panulirus regius* extends from the Gulf of Guinea southward along the northern part of the region and extends just to the southern part of Angola; however, it is nowhere abundant and although small quantities are presumably taken along the Angolan coast it does not appear in the catch statistics, and quantities must be presumed negligible. At Ascension Island and at St. Helena, offshore Atlantic islands which fall within this region, small stocks of *Panulirus echinatus* occur, and although these may have been fished in the past the quantities produced are negligible. Further to the south, at Tristan da Cunha and at Vema Seamount, stocks of *Jasus tristani* occur; the recent discovery of the stocks of this species on Vema Seamount, which is some 500 mi to the northwest of Cape Town has led to the development of a very active fishery there. Production figures for these offshore stocks were not, however, available to the Working Party.

Along the coasts of Southern Africa between Walvis Bay and Cape Agulhas, there are rather large stocks of *Jasus lalandii* which have been exploited for many years, and which are under strict management control. In the Indian Ocean, along the coast of Natal considerably smaller quantities of the Natal rock lobster *Palinurus gilchristi*, and *Panulirus homarus* and also some *P. versicolor*, and *P. ornatus* occur. Production figures for spiny lobsters from southern Africa in the last few years are tabulated below.

ROCK LOBSTER PRODUCTION IN SOUTHERN AFRICA IN RECENT YEARS (TONS × 10^3)

	Jasus lalandii		*Palinurus gilchristi*
	*Luderitz area**	*Cape Atlantic Coast*	*Natal Coast†*
1961	—	3.11	0.06
1962	—	3.02	0.07
1963	5.9	3.11	0.08
1964	7.6	3.11	0.18
1965	8.0	3.11	0.28
Total, 1965 = 11.4			

* FAO statistics

† S.A. Department of Commerce and Industry Statistics

The management data for *Jasus lalandii* suggests that the stocks of this species around Southern Africa are presently fully exploited; evidence from steadily decreasing average size and steadily decreasing catch per unit effort support the supposition that production from known stocks of *Jasus* in southern Africa will not be significantly increased. In fact, in recent years pressure has been brought on the government's quota system for production of *Jasus* by the fishing companies in response to their diminishing returns. The discovery of new grounds, as at Vema Seamount, and the steadily increasing rate of production on the Indian Ocean coast of southern Africa will to some extent help the situation but it is thought that none of these resources will significantly relieve the pressure upon the main stocks of *Jasus lalandii*, which are concentrated to the west of Cape Agulhas.

B. *Prawn and shrimp resources*

Exploratory fishing off southern Africa for shrimps and prawns in recent years has been relatively profitless though finds of commercial quantities of large penaeid prawns (*Penaeus* sp. and *Hymenopenaeus triarthrus*) were made in depths of almost 250 fm at the edge of the southern African continental shelf together with good quantities of a species of *Solenocera*. Also present on these grounds, which are to the east of Cape Agulhas and off Natal, are *Nephrops andamanicus* and the Natal rock lobster.

There are small prawn fisheries in existence along the coast of Natal where, in 1966, about 90 metric tons were landed at Durban, and a few more tens of tons by a group of inshore fishermen at Santa Lucia; however it is assumed that most of the catches landed at Durban have been taken off the coast of Mozambique, which have been discussed with under Region VII. The species involved in the landings at Durban are the following: *Penaeus indicus*, *P. monodon*, *P. japonicus*, *Hymenopenaeus triarthrus*, and *Aristaeomorpha foliacea*; of these, about 70% probably is made up of a single species (*Penaeus indicus*) to judge from the specific composition of the prawn stocks off Mozambique. Lesser quantities, which are often not marketed, of *Metapenaeus monoceros*, *Plesionika martia*, and *Chlorotocus crassicornis* are also taken. *Penaeus indicus* is the most important species taken by inshore fishermen in Natal, with *P. japonicus* second in importance in southern Natal and *P. monodon* and *M. monoceros* about equal and second in importance in northern Natal.

Along the coast, north of Walvis Bay as far as the Kunene River there are very abundant stocks close inshore of the small prawn *Macropetasma*, which have been revealed by trawling surveys in this region; however, no commercial exploitation of them appears to have yet occurred.

Towards the end of 1966 a new fishery for prawns and shrimps was developed off the coast of Angola; this was initiated by the arrival of a single Spanish trawler skilled in trawling for deep water prawns in the western Mediterranean out of the port of Huelva. By the beginning of 1968, this vessel had been so successful that a small fleet of 40 trawlers (from 30–50 m overall) had built up in the Angola region, most of them from Spain and principally from the ports of Vigo, Huelva and Cadiz. These vessels are presently making campaigns of about 8 months in the region, and it appears that the annual production now exceeds 1,000 metric tons.

The species of shrimp fished are the gamba, *Parapenaeus longirostris*, the listado, *Aristeus varidens*, and the carabinero, *Plesiopenaeus edwardsianus*. These excellent, large prawns (gamba reach between 9 and 18 cm, listado reach 19 cm and carbinero almost 30 cm) are taken from 6°50′S to 12°S, and in a rather narrow, but deep, depth zone; throughout this region gamba are taken from 250–260 m and the other two from 540–600 m in depth. In this area the slope of the continental shelf is rather steep and the trawlers follow a very narrow band of contours which gives them certain practical problems. It will be noticed by reference to the section upon Region III, and the Mediterranean and Black Sea, that species taken off Angola are identical with species which are also important in the western Mediterranean; this is an expression of the very similar fauna which occurs throughout the tropical Eastern Atlantic at depths below the break of slope on the continental shelf, and which contains very many species in common with the Mediterranean Sea and the coast of western Europe as far to the north as Ireland. In assessing the potential production from this region, it is certainly reasonable to assume an increase in production by a factor of ×2 or ×3 and it seems very probable that the total production of shrimps and prawns between South Africa and Angola inclusive could very easily reach a level of 5.0×10^3 tons, which estimate is used here. Also not included in the present consideration are four deep-water penaeids (*Aristaeomorpha foliacea*, *Aristeus varidens*, *Penaeopsis serrata*, and *Plesiopenaeus edwardsianus*) and the pandalid *Plesionika edwardsii* have been reported on numerous occasions as occurring throughout the area but none of these except *Penaeopsis megalops* (which is of small size) has been located in concentrations sufficient to suggest supporting a commercial fishery. These species, therefore, have not been included in the estimates. The following tabulation summarizes the present production of prawns throughout the area by countries, and their estimated potential production. This cannot be broken down by species as in almost every case the available statistics do not permit this.

	Present (tons × 10^3)	*Potential*
Congo to Kunene *Parapenaeus longirostris*, etc.	1.0	5.0
Kunene to Orange *Macropetasma* sp.	—	1.0(?)
Natal Coast *Natal penaeids*	<1.0	1.0(?)
Total	<2.0	7.0

C. *Total potential of Region XII*

The data discussed in the text above do not suggest that this region will become a major producer of crustacea in global terms; the tabulation below indicates the likely magnitude of potential production in the foreseeable future.

	Present (tons × 10^3)	*Potential*
Lobsters		
Jasus lalandii	10.4	10.5
Palinurus spp.	0.3	1.0(?)
Prawns		
Congo to Kunene	1.0	5.0
Kunene to Orange	—	1.0
Orange to Limpopo	<1.0	1.0
Total	12.7	18.5

Region XIII—Southwest Pacific

Region XIII comprises Australia (except W. Australia), New Zealand and its contiguous islands, including New Caledonia and New Hebrides. Exploitation of prawns and crawfish is actively pursued by local fleets, and also by Japanese and Soviet fleets, especially in the tropical northern parts of the region.

A. *Spiny lobsters*

Various species of spiny lobsters or crawfish are important exploited resources of New Zealand, and of the southern part of Australia.

New Zealand

Southern crawfish (*Jasus edwardsii*) has been under exploitation for many years by small vessels out of most New Zealand ports, especially those with access to the west coast grounds. Landings in recent years have been:

(tons × 10^3)	
1962—4.6	1965—5.0
1963—4.6	1966—6.6
1964—4.6	

For many years the catches have been increasing steadily due mainly to exploitation of fresh grounds on a continuing basis. The sudden increase in 1966 was due entirely to extension of fishing onto the banks around the Chatham Islands, away to the east of the main islands.

Southeast Australia

The southern crawfish (*Jasus novaehollandiae*) is the principal species fished, but others occur, among them the painted crawfish (*Panulirus versicolor*), not presently taken because of its unwillingness to enter pots.

As the following catch statistics show, none of the eastern or southern states enjoy such heavy landings of crawfish as are taken in western Australia (see Region VIII), where *Panulirus cygnus* yields 7.0 to 8.0×10^3 tons per year.

Catches in recent years of *Jasus lalandii* off Australia:

	1964–65	*1965–66* (tons × 10^3)	*1966–67*
New South Wales	0.2	0.2	0.2
Queensland	+	+	+
Victoria	0.6	0.7	0.7
Tasmania	1.5	1.8	2.0
South Australia	2.7	2.7	2.8
Total	5.0	5.4	5.7

The slowly rising catches in Australia and the rapidly rising catches in New Zealand, both in fisheries with rather rigid management policies, suggest that in neither place are the stocks fully exploited; in particular, it is likely that the opening of the Chatham Island grounds will further increase New Zealand's catches significantly.

Any catches by foreign vessels in those regions are not available, and any quantification of total potential yields from this region are to this degree uncertain.

B. *Crab resources*

Small quantities of several species of crabs are taken in Australia, not totalling as much as 1.0×10^3 tons, and these catches are ignored here. Future potential of the stocks is entirely unknown. Spider crabs (*Jaquinotia edwardsii*) seem to offer fair prospects around Auckland I.

C. *Prawn resources*

Between 40 and 50 species of penaeid prawns occur in the region, and of these about 10 are presently useful in the fisheries; many smaller species of shrimps and prawns belonging to other decapod groups also occur, of course, and while some may have local or limited usefulness in the future there are no indications from present data that any will approach the value of the penaeids.

In Australia, exploitation is most complete near the southern and eastern centres of population, and is expanding most rapidly in the under-populated northern regions; off New Zealand, several recent surveys have shown no indication of major prawn resources. A number of species of penaeids occur, and *Nephrops challengerii* has been found in promising quantity in deep water (over 150 fm, 300 m).

Queensland

A trawl fishery operates along the continental shelf from Cairns south to the border of New South Wales, and landings are made in all ports of this area. Five species are exploited: *Penaeus plebejus* (65%), *Metapenaeus bennettae* (16%), and *P. esculentus*, *P. merguiensis* and *M. macleayi* (19%). *P. plebejus* is taken throughout the year, the others during more restricted summer seasons.

Production figures are slowly rising, mainly due to increasing exploitation of oceanic stocks of *Penaeus plebejus*, as tabulated below:

(tons × 10^3)	
1962—2.0	1965—2.6
1963—2.3	1966—2.7
1964—2.3	1967—2.7

The future of this fishery is presently unsure, since although a very limited increased production may be possible from the stocks of *P. plebejus*, the stocks of the other species already appear to be overfished.

A set-net fishery in the Moreton Bay rivers of Queensland takes small quantities of *Metapenaeus bennettae*, but this is not separable in the statistics and is included in the figures given above for the trawl fishery, as are the catches from a variety of small-boat trawls and hand-nets in the estuaries and brackish lagoons, where the catch is mainly of *Penaeus plebejus*, *Metapenaeus macleayi* and *M. bennettae*.

New South Wales

The trawl fishery discussed above extends southwards along much of the coast of New South Wales, at least as far as the port of Terrigal, the fleet being dispersed among many of the small ports.

The available statistics for this area do not permit partitioning the catch between the five species involved, which are identical to those in the catches off Queensland. The available data, tabulated below, show that peak production has probably already been achieved in this fishery and no significant increase can be expected from natural resources in the future:

(tons × 10^3)	
1963—2.1	1965—2.0
1963—3.0	1966—1.8
1964—2.8	1967—1.8

As in Queensland, catches from the estuarine and lagoon fishery and from a small pocket set-net fishery in lagoon channels, are included in the above data; the same species are exploited as in Queensland.

There appears to be no likelihood that the catches off New South Wales can be increased and present management policies are presumably designed to maintain the present yield; off Queensland, a modest increase is likely, mainly of oceanic *Penaeus plebejus*, but there appear to be no data on which to make a quantified estimate, though a figure between 10% and 20% over present catches seems not unreasonable.

D. *Total potential of Region XIII*

Only in the case of the tropical shrimp resources of Australia are there any known predictions by local fisheries agencies of the potential size of the catches of crustacea in the region. It seems reasonable to apply subjective, order-of-magnitude extrapolations to fisheries according to the trend of the catches in recent years so as to reach some estimate of the total potential in the whole region. This is done in the following tabulation:

	Present	*Potential*
	(tons × 10^3)	
Crawfish		
New Zealand	6.6	8.2
S.E. Australia	5.7	6.3
	(12.3)	(15.4)
Crabs		
Australia	<1.0	<1.0
	(1.0)	(1.0)
Prawns		
New Zealand	—	—
Queensland	2.7	3.1
New South Wales	1.8	1.8
	(4.5)	(4.9)
Total	17.8	>20.3

This estimate of potential catches ignores the possibilities where no fisheries now exist, or where no resource surveys have been performed. It is certain that some potential in tropical crawfish occurs on the offshore reefs of the Queensland coast, and off New Caledonia and New Hebrides, both of which currently report no fishing and no potential for crustaceans. It would probably be safe to add another 5.0 × 10^3 tons for such completely hypothetical resources, raising the grand total for the area to around 25.0 × 10^3 metric tons, in the long-term.

Region XIV—Southeast Pacific

The coasts of Peru and Chile fall within this region; though rich because of strong coastal upwelling, the narrow shelf and the generally rocky nature of the coast is rather unsuitable for the development of great crustacean resources, especially of prawns or shrimps.

A. *Crab resources*

Lithodes antarcticus has formed the basis of a small fishery in recent years which has shown a modest rate of increase in production, and which now approaches 500 tons per year (see tabulated data below); this is an ecological analogue of the king-crab of the North Pacific (*Paralithodes camtschatica*) which yielded catches approaching 150.0 × 10^3 tons. Although (i) the shelf area on which *Lithodes antarcticus* is known to occur is very much less than that for the northern form, and (ii) the southern form averages less than 2 kg against 4 kg for the northern form, it still seems possible that an expansion in this fishery will develop in southern Chile's region of fjords and offshore islands: an increase by a factor of 2–3 seems not unlikely and will be used here, and it is suggested that the potential catch is at least 1.5 × 10^3 tons per year.

Other species (*Cancer* spp., *Taliepus* spp., and *Homalaspis* spp.) of crabs form the basis of a fishery which is presently considerably larger than that for *Lithodes*, and which yields a little less than 1.5 × 10^3 tons annually in Chile and about 0.2 × 10^3 tons in Peru. There is no evidence to suggest that this fishery is capable of expansion, but in view of the great length of Chile's indented coastline and the present extent to which the fishery is concentrated near centres of population, a factor of 10 is applied for potential production. It is, therefore, suggested that at least 15.0 × 10^3 tons may eventually be taken by that fishery each year.

Galatheids of two species (*Pleuroncodes monodon* and *Cervimunida johni*) support a Chilean fishery which is to some extent complementary to that for prawns. The same vessels fish each stock and the landings of galatheids and of prawns vary inversely. In recent years the catches of galatheids have been ranging from 10.0 to 13.0 × 10^3 tons per year, and it is evident from surveys of the abundance of galatheids on parts of the shelf off Chile and Peru influenced by deposition of material from phytoplankton blooms that an increase of at least a factor of ×5 seems possible. This places the potential catches from these stocks at around 50.0 × 10^3 tons annually. Meat yield is rather low from galatheids, however, and this represents a total of only about 5.0 × 10^3 tons of tails.

B. *Spiny lobster resources*

Small stocks of spiny lobsters occur, the most important species being *Jasus frontalis*, which occurs especially at the offshore islands (e.g. Juan Fernandez) but does not seem to occur on the mainland. The data tabulated below shows the small size of this production and suggests that the potential yield may not be much in excess of 0.1 × 10^3 tons per year.

C. *Prawn resources*

A fishery based on *Heterocarpus reedi* and *Rhincocinetes typus* yields about 11.0 × 10^3 tons in Chile and about 0.5 × 10^3 tons in Peru annually. Resource surveys of the grounds on which the species occurs in commercial quantities indicate that these have an extent of 1,600 km², and do not extend below 37°S. The grounds are heavily exploited near ports, but rather lightly farther away from markets, and an increase by a factor of 2 for a total of around 20.0 × 10^3 tons potentially, seems very probable.

A second species, *Hymenopenaeus diomedeae*, has been surveyed, but is not yet exploited commercially. Occurring rather deeply, at >150 fm, it has not been easy to estimate its potential yield, or the extent of its occurrence satisfactorily. Exploitation will be possible only when production problems imposed by the nature of its habitat are solved, and for present purpose a conservative estimate of 1.0 × 10^3 tons is placed on its potential yield.

ANNUAL RATE OF PRODUCTION OF CRUSTACEA BY CHILE, 1961–66
(tons × 10^3)

	Lithodes	*Crabs*	*Galatheids*	*Spiny lobsters*	*Prawns*	*Barnacles*
1961	0.2	1.0	8.1	0.1	2.3	0.5
1962	0.3	0.9	7.9	0.1	4.3	0.9
1963	0.1	0.9	9.2	0.1	3.6	1.5
1964	0.3	1.0	10.6	0.1	5.9	1.0
1965	0.3	1.3	13.3	0.1	5.0	1.5
1966	0.4	1.3	11.3	0.1	10.9	0.9

D. *Barnacle resources*

Chile is unique in its exploitation of the giant barnacle, *Balanus* (*Megabalanus*) *psittacus* which reached 2.0 × 10^3 tons in 1954, but is lightly fished and market-limited, so that in some recent years only 1.0 × 10^3 tons were taken. It may reasonably be expected to yield 5.0 × 10^3 tons potentially.

E. *Total regional potential yield*

This may be expressed as:

	Present (tons × 10^3)	*Potential*
Crabs	14.2	66.5
Spiny lobsters	0.1	0.1
Prawns	11.5	20.0
Barnacles	1.0	5.0
Total	36.8	91.6

But it must be emphasized that this potential increase, by an overall factor of almost ×3, is based on extremely subjective judgments, and must not be taken in any other light.

GLOBAL ASSESSMENT

The tabulation below summarizes the 14 regional assessments presented in the body of the text.

It shows that on the descriptive evidence and on the quantitative data available for this review, the world catch of crustaceans, presently about 1.26 × 10^6 tons, may be expected to rise in the future to almost double this figure, or 2.31 × 10^6 tons annually. This estimate supposes that no "break-throughs" in harvesting technology which cannot now be foreseen will occur, and that in consequence the resources to be exploited will be similar to those we exploit today.

Summarized tabulation of present and potential world production of crustacea (tons × 10³)

	Region	Present			Potential		
		Lobsters	*Crabs*	*Prawns*	*Lobsters*	*Crabs*	*Prawns*
I	Northwest Atlantic	31.7	2.2	8.6	32.0	10.0	27.0
II	Northeast Atlantic	29.9	13.3	65.4	65.3	20.5	82.8
III	Mediterranean	4.0	+	23.0	4.0	+	50.0
IV	North Pacific	+	208.0	41.1	—	250.0	131.2
V	Western Central Atlantic	13.3	76.9	125.0	21.0	80.0	160.0
VI	Eastern Central Atlantic	2.5	+	4.6	4.0	10.0	63.0
VII	Western Indian Ocean	0.4	+	21.3	3.1	+	144.0
VIII	Eastern Indian Ocean	8.6	+	58.9	10.0	+	98.1
IX	Western Central Pacific	1.7	39.3	304.1	5.0	150.0	544.1
X	Eastern Central Pacific	+	<1.5	65.0	5.0	32.5	75.0
XI	Southwest Atlantic	3.5	15.8	37.1	4.0	21.0	86.0
XII	Southeast Atlantic	10.7	+	2.0	11.5	+	7.0
XIII	Southwest Pacific	12.3	1.0	4.5	14.5	1.0	4.9
XIV	Southeast Pacific	0.1	14.2	11.5	0.1	66.5	20.0
	Total	118.7	372.2 (1.26×10^6)	772.1	179.5	641.5 (2.31×10^6)	1,492.1

This final tabulation invites some discussion of the implications it contains of the degree of exploitation of the various resources, and also of the relative validity of the estimates which it comprises.

It is evident from the lack of quantitative data that crab resources, with a few notable exceptions, are either largely ignored, or are treated as of such small importance, that they are lost in statistical "catch-alls" and recorded only as "miscellaneous crustacea" or some similar category. It is probably in this general group of resources that both our estimates of present production, and our prognostication of how trends in harvesting will run in the future, are poorest. In the final estimates there is a very large component of subjectivity; the numbers used in this table, however, from the nature of the doubts expressed here, will be minimal and are likely to be exceeded by reality, rather than the opposite.

It is probably also an indication of this data problem, and hence of the great difficulty of making predictions, that makes the apparent percentage increase in production which the table suggests to be rather low.

On the other hand, the quantitative data for all forms of lobster-like crustaceans reflect the high esteem with which these animals are held in world markets. In most cases, the figures used here are rather reliable and the modest size of the increase in production which appears to be possible is probably just a measure of the high intensity of exploitation, and of management, to which stocks of "lobsters" are already subjected.

The quality of the data which are available for prawns and shrimps is extremely variable: in such places as the Gulf of Mexico and the Eastern tropical Pacific Ocean it is very good, while for some resources (such as the deep penaeids and pandalids) the data are very incomplete, and for several regions (such as the Eastern Indian Ocean) they are very subjective.

Perhaps the two areas of greatest uncertainty in estimations of prawn resources concern the deep red prawns on the upper parts of the continental slope, and the stocks of small, brackish water carideans, especially in the tropics.

Although prawns of rather a small number of species and genera, typically having rather great areas of distribution, have apparently been found whenever looked for below the continental edge in low and middle latitudes, these are exploited in only three areas; the Gulf of Mexico, the Mediterranean and off Angola. While the Angolan experience in recent years shows that substantial production can be achieved from these resources, there are presently no data on the biological parameters required to judge what sort of sustainable yield may be taken from presently almost virgin stocks. Nor are the survey data elsewhere, for instance in the Eastern Indian Ocean, sufficiently quantitative to compare prospects elsewhere with production in the Mediterreanean or off Angola.

The appearance in the production statistics for the western coast of Indian of 35.0×10^3 tons of small caridean shrimps is very surprising in terms of other similar regions. The coast in question is not typical of tropical regions, but is significantly distinguished by the excellence of the statistical reporting system at the village level, and it must be supposed that similar catches could be (or are) made in parts of the Gulf of Guinea, in the Indonesian and Philippine archipelagos and along northern Australia. Such suppositions appear to be rather poorly supported by the available quantitative data.

Appendix

TABLE R1. CATCHES OF CRUSTACEANS BY SPECIES AND BY COUNTRIES ('000 METRIC TONS, LIVE WEIGHT)

Species	*Country*	1958	1963	1964	1965	1966	1967	1968	1969
Sea-spiders, crabs, etc.		197.0	272.0	288.0	318.0	365.0	368.0	388.0	397.0
Blue crab		50.0	66.0	71.0	78.0	77.0	68.0	58.0	68.0
Dungeness crab		21.0	13.0	13.0	15.0	20.0	22.0	25.0	24.0
Edible crab		10.0	10.0	10.0	8.0	8.0	8.0	8.0	10.0
King crab		64.0	110.0	117.0	130.0	150.0	131.0	112.0	86.0
	USA (Pacific)	5.1	35.7	39.3	59.7	72.3	57.9	37.2	25.3
	Japan	28.2	31.6	31.8	25.9	31.0	30.3	30.4	22.5
	USSR	30.9	42.5	46.2	44.4	46.0	42.3	40.4	37.1
Other marine crabs		52.0	73.0	77.0	87.0	110.0	139.0	185.0	209.0
	Japan	30.9	39.6	42.0	37.7	40.7	55.9	87.5	70.9
Lobsters, rock lobsters, spiny lobsters, etc.		79.0	90.0	92.0	92.0	92.0	88.0	96.0	...
European lobster		4.0	3.0	5.0	3.0	2.0	2.0	2.0	2.0
Northern lobster		32.0	34.0	33.0	32.0	30.0	28.0	32.0	34·0
Spiny lobster, rock lobster		43.0	53.0	53.0	56.0	59.0	57.0(a)	(61.0)	...
	Namibia	4.0	5.9	7.6	8.0	8.9	5.9	8.5	...
	South Africa	12.7	8.3	8.4	8.4	8.0	8.3	6.7	...
	Cuba	4.2	7.4	6.6	9.1	9.0	8.3	8.9	11.1
	Brazil	1.1	3.6	3.3	3.4	2.8	2.5	3.2	6.3
	Australia	10.0	14.3	12.6	11.9	13.6	14.4	15.1	13.0
	New Zealand	4.4	4.5	4.6	5.0	6.6	8.1	10.9	8.9
Squat-lobsters, nephrops, etc.		32.0	38.0	41.0	43.0	45.0	51.0	50.0	59.0
Squat-lobsters		13.0	9.0	11.0	15.0	13.0	20.0	18.0	24.0
Norway lobster		19.0	29.0	30.0	28.0	32.0	31.0	32.0	35.0
Shrimps, prawns, etc.		502.0	671.0	670.0	663.0	697.0	757.0	771.0	...
Common shrimp		49.0	73.0	57.0	51.0	60.0	45.0	50.0	47.0
	Germany (Fed. Rep. of)	29.4	42.4	28.7	28.3	38.4	24.3	33.1	27.6
	Netherlands	13.1	24.7	21.9	17.4	15.5	14.3	11.2	11.7
Deep-water prawn		13.0	26.0	23.0	25.0	21.0	22.0	23.0	24.0
Prawns and shrimps		440.0	572.0	590.0	587.0	616.0	690.0	698.0	...
	Mexico	50.2	72.0	69.0	59.1	65.8	70.1	58.6	54.7
	USA (Atlantic)	88.9	99.4	89.5	101.4	92.8	114.9	110.2	115.4
	USA (Pacific)	8.1	9.6	6.6	9.1	15.6	24.7	25.6	28.4
	Brazil	17.4	28.3	28.1	39.4	34.7	35.5	39.5	36.7
	China (Taiwan)	4.0	9.0	9.8	14.2	16.3	19.5	25.6	34.4
	India	86.7	81.6	94.9	77.2	90.8	91.7	99.8	107.6
	Japan	55.6	86.7	77.8	66.5	68.8	61.0	70.7	61.2
	Korea (Rep. of)	16.4	14.2	18.1	17.2	12.1	21.0	11.4	6.8
	Malaysia (West)	9.0	19.0	19.3	20.8	24.4	32.3	32.9	39.4
	Pakistan (b)	14.9	18.4	20.7	22.0	22.2	25.0	23.4	26.0
	Philippines (c)	13.7	20.3	21.5	22.9	26.3	24.0	21.5	23.5
	Thailand	10.3	23.3	29.5	35.2	45.3	61.7	75.0	77.1
Miscellaneous marine crustaceans		36.0	53.0	67.0	69.0	77.0	102.0	106.0	...
Total, all crustaceans		860.0	1,140.0	1,170.0	1,190.0	1,280.0	1,360.0	1,400.0	...

Notes: (a) In the computation of this total, more than 10% was estimated by FAO
(b) 1958, "Prawns and shrimps" includes "Freshwater crustaceans"
(c) Up to 1966, "Prawns and shrimps" includes "Other marine crabs"
... No data
Brackets denote estimation

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7130

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Breeding in an Oceanic Population of *Pleuroncodes planipes* (Crustacea, Galatheidae)[1]

ALAN R. LONGHURST[2] AND DON L. R. SEIBERT[3]

ABSTRACT: The pelagic population of *Pleuroncodes planipes* known to occur in the California Current Extension is partly recruited by drift of megalopas from neritic regions and partly, as demonstrated by EASTROPAC samples, by breeding *in situ*.

THE DISTRIBUTION of pelagic adults and larvae of the galatheid crab *Pleuroncodes planipes* in the California Current has been described recently (Boyd, 1963, 1967; Longhurst, 1967, 1968). These studies showed the regular occurrence of an oceanic population of small adults far beyond the normal neritic habitat and indicated how this expatriate population might be recruited from megalopas derived from the neritic population along the west coast of Baja California.

The Eastern Tropical Pacific (EASTROPAC) expeditions (February 1967 to March 1968 from 20° N to 20° S and from the American continent out to 126° W) afforded an opportunity to investigate this oceanic population and to test the hypothesis concerning its origin. The new data are derived from adult and larval *Pleuroncodes* sorted from the catches of 171 hauls with a 5 × 5 foot micronekton net (Blackburn et al., 1970), and 221 hauls with the standard EASTROPAC plankton net (Love, in press). Both were deployed in oblique hauls to 200 m depth.

The samples were arranged in two series: one to give coverage every 2 months of Areas 1 and 2 (Fig. 1) and the other to give coverage twice yearly (summer and winter) of Area 3. Diel migration of small individuals biased the relative numbers and size-frequency within day samples; only size frequencies of night samples are used here.

Adults of *Pleuroncodes planipes,* none of which had carapace lengths exceeding 15 mm, were found early in the year in northern Area 1. This population (carapace length 9 to 13 mm) shifted its locus in late summer until, at the end of the year, all occurrences were south of 14° N; the second winter cruise (February–March 1968) showed that the population had shifted north again to a locus between 14° to 20° N. In Area 2, adults were present only after August–September, when a population of very small (6 to 8 mm) adults appeared in the samples and remained through the end of the year.

Two populations of larvae of *Pleuroncodes planipes* were found in the samples, the first (in Area 1 in February–March 1967) being derived from *in situ* breeding. Of 2,211 adults in the samples from this cruise, 112, or approximately 10 percent of the females, were found to be ovigerous. These were all small, 1-year-old (Boyd, 1963) crabs, of carapace length 10 to 15 (mode 12) mm.

In February–March 1967, about half the plankton samples from Area 1 contained early larvae of *Pleuroncodes planipes* (stages I–II only, of Boyd, 1960), clearly derived from the local population of ovigerous females, since stage I larvae were found as far as 750 miles southwest of Cape San Lucas, Baja California. Stage I and II larvae were present in Area 1 through May and stage V larvae were found in June. In February–March 1968, early larvae were again found in central Area 1, suggesting that oceanic breeding in this region is a regular occurrence.

The second population of larvae appeared as megalopas in Area 2 in July and August, extend-

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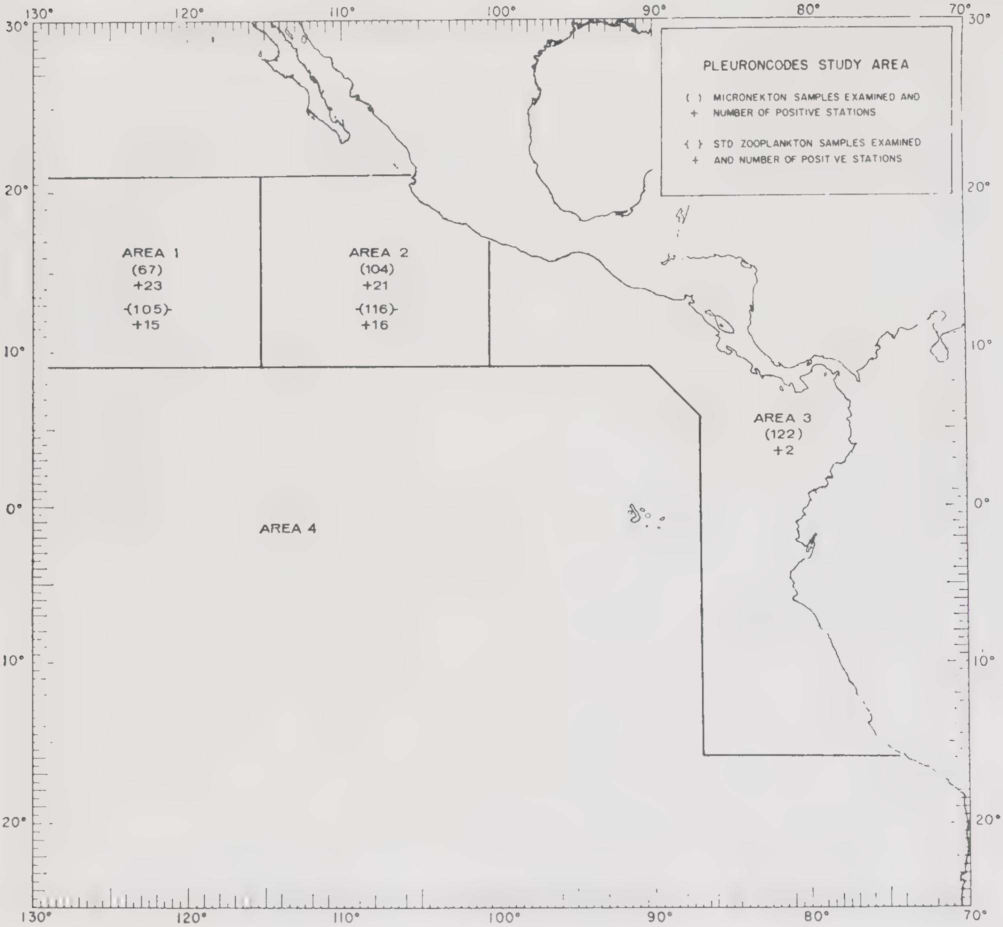
PLEURONCODES STUDY AREA
( ) MICRONEKTON SAMPLES EXAMINED AND
+ NUMBER OF POSITIVE STATIONS
{ } STD ZOOPLANKTON SAMPLES EXAMINED
+ AND NUMBER OF POSIT VE STATIONS
AREA 1
(67)
+23
{105}
+15
AREA 2
(104)
+21
{116}
+16
AREA 3
(122)
+2
AREA 4
130°
120°
110°
100°
90°
80°
70°
30°
20°
10°
0°
10°
20°

FIG. 1. The study area, and the numbers of micronekton and plankton samples sorted in Areas 1–3. An independent sorting for other purposes of about 650 micronekton samples in Area 4, north of lat. 20° S, turned up no further samples of galatheid crabs.

ing from the coast out to 112° W, and this population persisted through November, clearly giving rise to the very small (6 to 8 mm) adults mentioned above for this area in the latter part of the year. Monthly mean charts of surface current vectors (e.g., Wyrtki, 1965) suggest that this population of megalopas originated off southern Baja California or possibly in the Gulf of California.

In Area 3, 122 (micronekton net) samples were taken, and in only two of these was *Pleuroncodes* found; at one station off Central America and one off Peru, both in the southern summer, many *Pleuroncodes* megalopas were found, which were distinguishable from those of *P. planipes;* it is reasonable to assume that these belonged to *Pleuroncodes monodon,* the "langostino" of the Chile-Peru shrimp fisheries. Boyd (1963) suggested that this species might also occur off Central America, and this has recently been confirmed by specimens now in our possession from San Salvador and Costa Rica (Schaefer, personal communication) which came from a population present in commercial quantities off that coast. The megalopas and small adults (carapace 5 to 10 mm) of the two species can be distinguished by several characters, the clearest of which are the transverse rows of setae across the carapace; these are abundant, strong, and closely set in *Pleuroncodes planipes,* but thinner and more sparsely set in *P. monodon.*

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7131

On Potential Density in the Deep South Atlantic Ocean[1]

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ABSTRACT

There is a great contrast between the relative distributions of potential density referred to 0 decibars and of potential density referred to 4000 decibars in the deep water of the South Atlantic Ocean. Both parameters are useful in a descriptive analysis of deep water; the former is an identifier of water origin, the latter graphically displays stability in the deep ocean and can be used to infer deep-ocean geostrophic flow.

Introduction. In the South Atlantic there are large differences in the deep water characteristics of the basins flanking the mid-Atlantic ridge. Antarctic Bottom Water (AABW), characteristically cold and of low salinity, lies along the bottom of the Brazil Basin (western basin); the overlying North Atlantic Deep Water (NADW) is warmer and more saline. NADW fills the great depths of the Angola Basin (eastern basin) and is nearly homogeneous below 3500 m. The distributions of these characteristics are illustrated in zonal sections presented in atlases by Wüst (1935), who has used the 1925–1927 METEOR data, and by Fuglister (1960), who has used the 1957–1958 International Geophysical Year data. Wüst has also presented sections of the distribution of σ_t; however, the usefulness of this density parameter in analyzing the deep water is doubtful. In this study a zonal section determined from the IGY data is examined in terms of (i) potential density[2] referred to 0 decibars,[3] σ_0, and (ii) the potential density referred to 4000 decibars, σ_4. The distributions

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[2] The density parameter used is actually $\sigma = 10^3(\varrho - 1)$, where ϱ is the specific gravity, not density. Density in g/cm^3 is slightly greater than ϱ, but the term "density" is preferred over "specific gravity" for brevity of expression and to remain compatible with earlier usage.

[3] The usual symbol is σ_θ. The newer notation is chosen to be compatible with the subsequent use of σ_4, in which the subscript specifies the reference pressure in decibars $\times 10^{-3}$.

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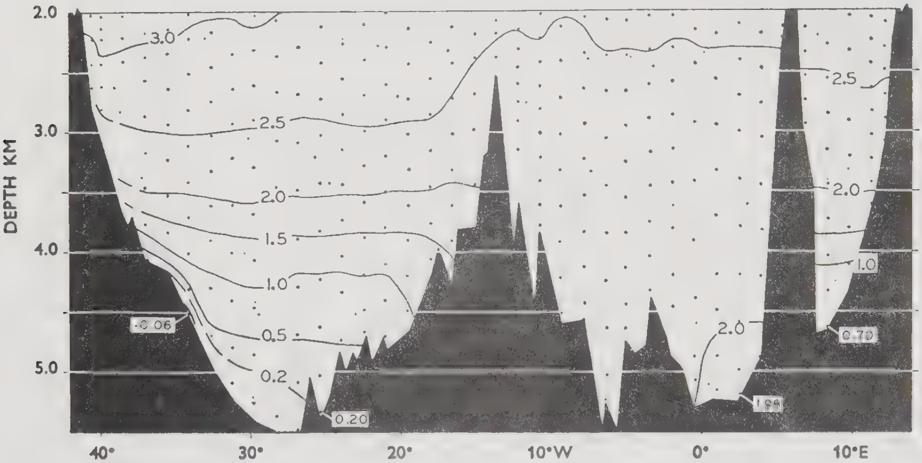

Figure 1. Potential temperature (°C) at depths greater than 2000 m in a section along 24°S in the Atlantic Ocean. The contour interval is 0.5°C except for the dashed line. The major topographic features are South America on the left, the Mid-Atlantic ridge, the Walvis Ridge, and Africa on the right.

of these parameters are useful in a descriptive analysis of the deep water and supplement the temperature and salinity distributions.

In a study of deep and abyssal waters of the world ocean, Lynn and Reid (1968) have presented vertical sections of σ_0 and σ_4 for a nearly meridional line of stations through the western Atlantic. The distribution of σ_0 in the deep ocean has revealed an internal maximum that helps to characterize a water mass and to identify its source and path of flow. However, these authors concluded that, to adequately represent the density stratification in deep water, potential density should be referred to appropriate pressures; the distribution of σ_4 eliminated the inversion and clarified the changes in density along the bottom.

Temperature and Salinity. The zonal section at 24°S, derived from data taken on R/V CRAWFORD Cruise 22, 1958 (Fuglister 1960), crosses the core of the AABW as revealed by the potential-temperature and salinity isopleths. At this latitude the AABW is banked against the western side of the Brazil Basin (Figs. 1, 2). At the bottom, the salinity is 34.67 to 34.69‰ and the potential temperature is near 0°C. (The temperature section referred to here differs from the one given by Fuglister (1960) in that he used *in situ* temperature.) The great overlying salinity maximum, near 2300 m, is approximately 34.94‰ and the corresponding temperature is approximately 2.9°C. The deep water in the Angola Basin, in great contrast to that in the Brazil Basin, is nearly homogeneous. Below 3500 m the vertical trends in salinity are nearly imperceptible; the median is 34.891‰. The potential temperature at the bottom is approximately 2.0°C and differs from that at 3500 m by 0.1°C.

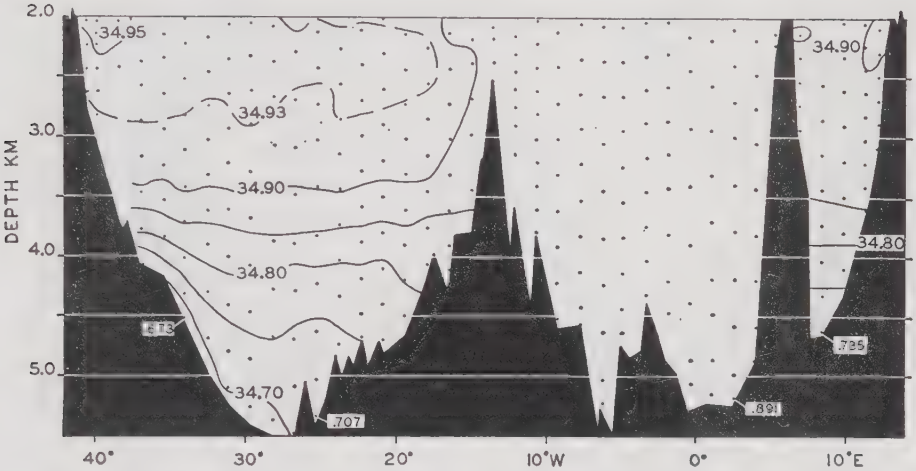

Figure 2. Salinity (‰) at depths greater than 2000 m in a section along 24°S in the Atlantic Ocean. The contour interval is 0.5‰ except for the dashed line.

The potential temperature and salinity at the bottom in the Cape Basin east of the Walvis Ridge are less extreme than those in the Brazil Basin, but they also exhibit the influence of AABW.

Potential Densities σ_0 *and* σ_4. In the deep Atlantic, σ_0 has a very weak gradient (Fig. 3). An internal σ_0 maximum is spread across most of the Brazil Basin near 3500 m and has about the same values (slightly greater than 27.90) as the waters below 3800 m in the Angola Basin. A faint σ_0 maximum (greater than 27.88) is found near 3500 m in the Cape Basin. Waters having these high values of σ_0 are part of the NADW and are traceable by means of this extreme characteristic to a latitude north of 40°N in the western North Atlantic (Wüst 1933, Lynn and Reid 1968, Reid and Lynn, in press). The AABW, though having lesser values of σ_0 than NADW, is colder, hence more compressible; and at the great pressures in the deep ocean it is more dense than NADW. In this zonal section the water column is everywhere stable.

The potential density referred to 4000 decibars (σ_4) increases monotonically to the bottom. The σ_4 density has a considerably larger gradient than σ_0 (Fig. 4); the contour interval used for σ_4 is five times greater than that used for σ_0. The AABW is the densest, and the least-dense bottom water is in the Angola Basin. Here and in the meridional section (Lynn and Reid 1968), the σ_0 maximum coincides closely with the 45.93 σ_4 isopycnal, which is nearly level across the Brazil Basin. In the AABW the σ_4 isopycnals parallel the potential-temperature and salinity isopleths.

There is a large difference in the relative distribution and in the gradients between the potential densities referred to 0 and to 4000 decibars. The rele-

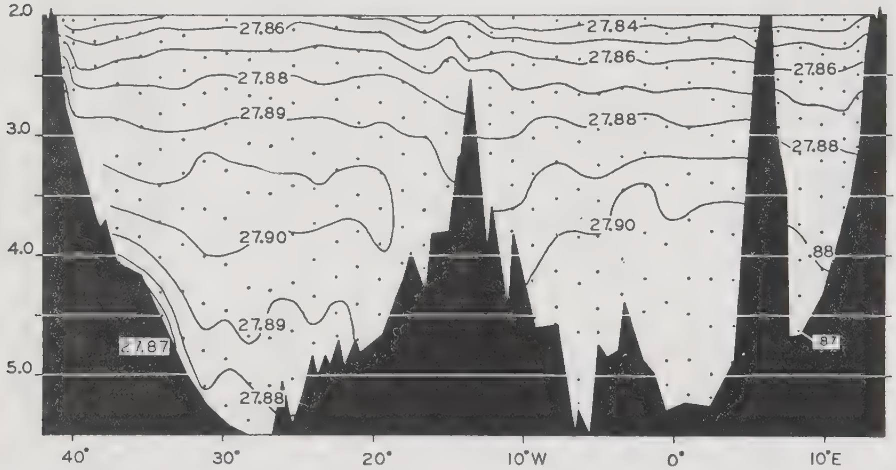

Figure 3. Potential density referred to a hydrostatic pressure of zero (symbol σ_0 or σ_θ) for the temperature and salinity fields given in Figs. 1 and 2. Contour interval is 0.01.

vance of a potential density referred to a particular pressure depends on its use and interpretation. We have seen that σ_0 in the deep ocean can be used as a conservative characteristic to trace water-mass origin while σ_4 shows the deep ocean stratification. The latter feature is explained in the following consideration. In practice, the Hesselberg (1918) stability parameter, $E = (1/\varrho)\,(\delta\varrho/\partial Z)$, is applied to the incremental observations derived from Nansen bottles. The density difference, $\delta\varrho$, is taken between two vertically adjacent observations after the lower is adiabatically raised to the depth of the upper. Where this depth happens to be the depth at which the pressure is 4000 decibars (3932 m), $\delta\varrho$ and $\Delta\sigma_4 \times 10^{-3}$ are equivalent. Thus, at the depth of the reference pressure,

$$\frac{\partial\sigma_p}{\partial Z} \times 10^{-3} = \left(\frac{\delta\varrho}{\partial Z}\right)_p .$$

In the vicinity of this depth the relationship is approximate, becoming less accurate at increasing intervals from the depth. As an example for this section, Crawford St. 428 (27°W) has been examined: near 3000 m and again near 5000 m, $E = 7 \times 10^{-8}$. Estimated from the vertical gradient of σ_4, we have 8×10^{-8} and 6×10^{-8}, respectively. Thus, within an appropriate depth range, the vertical section of σ_4 shows a density stratification that graphically reflects the stability. (Between 2000 m and 2500 m there is a decreasing trend from west to east in temperature and salinity. In this depth range the σ_0 and σ_4 isopycnals have opposing zonal slopes in the central part of the basin. The σ_2 isopycnals, which represent better the density structure in this depth range, have a slope that is intermediate between the others, i.e., nearly level).

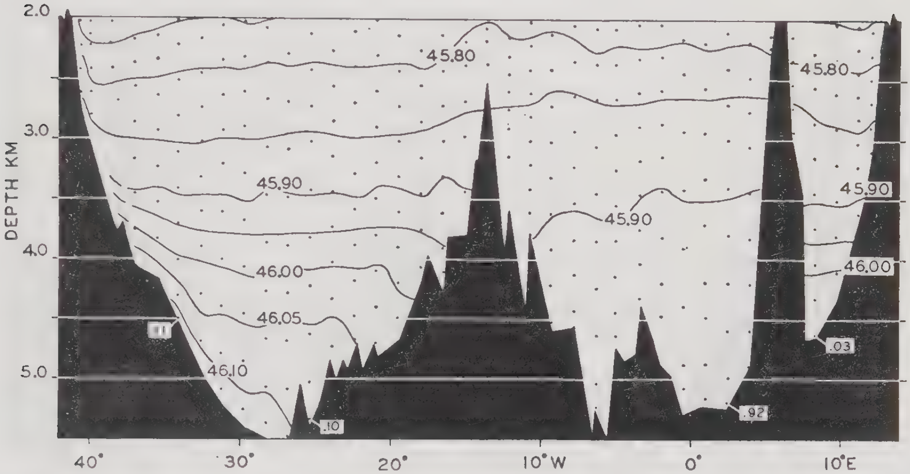

Figure 4. Potential density referred to a hydrostatic pressure of 4000 decibars (symbol σ_4) for the temperature and salinity fields given in Figs. 1 and 2. Contour interval is 0.05.

Deep Geostrophic Flow. The slope of the σ_4 isopyncals in the AABW suggest a mass distribution associated with geostrophically balanced motion. The horizontal density gradients below 4000 m in the Brazil Basin would be associated with a northward net motion in the bottom water relative to the overlying water. This is in agreement with the accepted pattern of circulation. (The horizontal gradients of σ_0 are of opposite sign, hence misleading). Wüst (1933, 1935) has described the deep circulation and the bottom circulation of the Atlantic as determined from the temperature, salinity, and oxygen distributions. Further, using the METEOR data, he analyzed deep and bottom geostrophic flow relative to Defant's "level of no-motion" (Wüst 1957, Defant 1941). In the South Atlantic he found northward flow of AABW along the western slope. At 24°S, Defant's "level of no-motion" varies at about a depth of 1200 m; the northward flow along the bottom (4000 m) was 3 cm/sec.

Geostrophic flow for the deep ocean was computed from CRAWFORD data relative to 3500 m–the depth of the σ_0 maximum–and relative to 1200 m. In the first calculation, the field of velocities (Fig. 5) relates the motion of AABW to an assumed no-motion in the overlying lower NADW, which may be moving southward. In this frame of reference, AABW has the only significant transport. The velocity increases with depth. The highest value (2.0 cm/sec) is located near the bottom; the calculation is limited in this critical region to computations for the depth of the shallowest of each pair of stations. The remainder of the field (velocities of less than 0.4 cm/sec not shown) shows lesser velocities, which often alternate their direction north and south between adjacent pairs of stations.[4] In the Brazil Basin the direction of flow represented by

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[4] Using the accuracies of the temperature and salinity measurements given by Fuglister (1960) for the IGY data (0.01°C and 0.005‰) and employing the methods of Wooster and Taft (1958), the

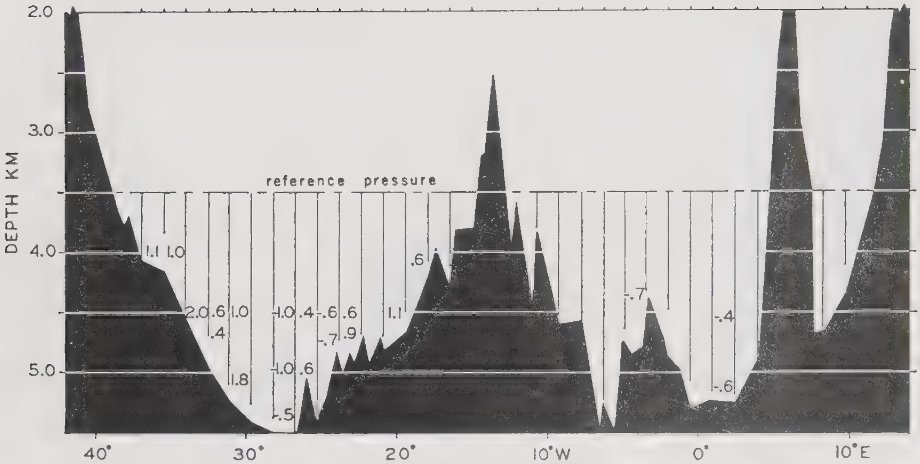

Figure 5. Geostrophic velocity (cm/sec) of the deep water relative to an assumed no-motion at 3500 m. Only values for 0.4 cm/sec and greater are given. Negative values indicate southward flow.

the larger values is still predictable from the σ_4 distribution. The velocities in the Angola Basin may be the result of small measurement errors. Two of the stations used in the determinations contain slight instabilities at great depth.

This analysis is intended to show that relative geostrophic motion in the near-bottom water is evidenced in the σ_4 distribution. It is probable, however, that the water at 3500 m is also in motion. Indeed, west of 25°W there is a southward flow of slightly less than 1 cm/sec at 3500 m if 1200 m is chosen as the reference level (not shown). In this second calculation, the vertical shear between 3500 m and near the bottom remains unchanged, hence the velocity of the AABW is reduced by the same amount. Higher velocities are found elsewhere; values greater than 4 cm/sec northward are found at 3000 m along the eastern edge of both the Brazil and Cape basins. However, it is difficult to infer geostrophic motion from the density field except where the horizontal density gradients are persistent across several stations.

Summary. Potential density is more descriptive of conditions in the deep ocean than has been popularly believed. For the South Atlantic section, and as seen in Lynn and Reid (1968), potential density referred to 0 decibars is an identifier of water origin. Referred to 4000 decibars, its distribution aids in the description of the water-mass distribution and circulation and shows a graphic display of the stability. Other potential densities are useful in other strata. The slopes of these isopycnals give the same indications of relative geostrophic flow as do the slopes of σ_t and σ_0 in shallower layers and are subject to the same limitations and interpretations.

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corresponding error in geostrophic current speeds for 24° latitude and 150-km station spacing is less than 0.5 cm/sec.

Acknowledgments. This paper represents one of the results of a project conducted jointly with J. L. Reid of the Scripps Institution of Oceanography. I wish to express my gratitude to J. L. Reid for his advice. Robert Owen and Merritt Stevenson also read the manuscript.

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7132

ADDITIONAL DATA ON THE SPAWNING OF THE HAKE

JOHN S. MACGREGOR[1]

ABSTRACT

In January 1970 samples of hake were taken off southern and central Baja California to study fecundity. In the southern area female hake as small as 130 mm standard length contained developing eggs, and all females longer than 140 mm contained such eggs. There is a marked cline in size at first maturity of hake along the Pacific Coast (hake in the Pacific Northwest exceed 400 mm before reaching maturity). Seventeen female hake 130 to 202 mm long taken in the southern area contained from 3,400 to 19,500 eggs or 229 per gram of fish; 11 females 222 to 305 mm from the central area contained from 3,500 to 110,000 eggs or 243 per gram of fish. In previously published data 22 female hake 346 to 688 mm from northern Baja California contained from 33,000 to 496,000 eggs or 192 eggs per gram of fish. There are no significant differences in fecundity among the three areas. The hake spawns once a year with over 98% of the spawning taking place between January and April.

In 1966, I published data on the fecundity of 22 female hake taken off northern Baja California. In 1970, additional samples of hake were obtained from central and southern Baja California to determine if there were geographic differences in hake fecundity in the offshore waters of Baja California.

The hake samples taken off southern and central Baja California in January contained prespawning females from which estimates of fecundity were obtained.

The hake from northern Baja California for which fecundity data have been published (MacGregor, 1966) appear to be identical to those taken off southern and northern California, while those taken farther to the south are different with respect to growth rate and size at first maturity and, in fact, have been described as a different species (Ginsberg, 1954).

The female hake for which fecundity determinations were made were taken by trawl from the research vessel *David Starr Jordan*. Station J-45-13 at lat 26°07′ N, long 113°07′ W was sampled January 11, 1970. Station J-45-27 at lat 28°44′ N, long 115°15′ W was sampled January 16, 1970. Methods for estimating fecundity of the samples were essentially the same as used previously (MacGregor, 1966).

Previous data on hake fecundity (MacGregor, 1966) were obtained from samples taken by the research vessel *John N. Cobb* (Berry and Perkins, 1966). Station C-58-23 at lat 31°49′ N, long 117°53′ W was sampled March 21, 1963. Station C-58-29 at lat 29°46′ N, long 116°01′ W was sampled March 23, 1963. Station C-58-31 at lat 29°35′ N, long 116°00′ W was sampled March 25, 1963.

FECUNDITY

The range for fecundity data for samples J-45-13 (Table 1) and J-45-27 (Table 2) compare with *Cobb* 1963 samples (MacGregor, 1966) as follows:

	J-45-13	*J-45-27*	Cobb *1963*
Standard length (mm)	130 to 202	222 to 305	346 to 688
Weight (g)	22.1 to 57.0	88.0 to 221.0	300 to 2,750
Gonad weight (g)	0.928 to 4.002	3.279 to 22.710	13.1 to 196.8
Advanced eggs	3,419 to 19,564	3,496 to 110,017	33,000 to 496,000
Eggs per gram of fish	141 to 343	38 to 498	83 to 556

There is no overlap in the ranges of standard length and fish weight of the samples from the three localities. The number of advanced eggs in the ovaries tends to increase with size of fish both within and between samples. However, because of the great variation in the numbers of advanced eggs among the individual fish, there is considerable overlap in gonad weight and numbers of advanced eggs between successive samples.

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Table 1.—Fecundity data for 17 female hake taken at Station J-45-13 (lat 26°07′ N, long 113°07′ W) January 11, 1970.

Standard length	Weight	Gonad weight	Gonad index	Advanced eggs		Eggs per gram of fish
				Size range	Number	
mm	*g*	*g*		*mm*		
130	22.1	0.928	4.2	0.50-0.67	3,419	155
131	23.3	1.345	5.8	.57- .73	7,049	303
135	25.2	1.320	5.2	.57- .77	3,564	141
137	22.4	1.518	6.8	.50- .67	6,469	289
137	29.3	1.795	6.1	.53- .70	7,139	244
138	24.8	0.987	4.0	.53- .70	4,048	163
140	28.8	1.350	4.7	.53- .70	4,956	172
140	34.5	2.241	6.6	.57- .77	7,926	230
141	30.5	1.222	4.0	.50- .70	4,534	149
150	21.2	1.198	5.7	.53- .73	4,257	201
150	37.1	2.481	6.7	.53- .73	10,864	293
160	31.5	1.875	6.0	.53- .73	6,447	205
162	30.3	1.957	6.5	.57- .73	7,633	252
170	32.3	2.000	6.2	.50- .70	8,741	271
172	37.7	1.863	4.9	.47- .70	10,731	285
174	37.7	2.000	5.3	.50- .70	7,559	201
202	57.0	4.002	7.0	.50- .67	19,564	343

Table 2.—Fecundity data for 11 female hake taken at Station J-45-27 (lat 28°44′ N, long 115°15′ W) January 16, 1970.

Standard length	Weight	Gonad weight	Gonad index	Advanced eggs		Eggs per gram of fish
				Size range	Number	
mm	*g*	*g*		*mm*		
222	100	8.663	9.7	0.50-0.67	29,399	294
230	88	7.011	8.0	.50- .73	23,253	264
233	104	8.488	8.2	.60- .77	29,450	347
238	91	3.279	3.6	.57- .73	3,496	38
245	105	6.292	6.0	.50- .70	17,511	168
247	120	5.956	5.0	.60- .80	18,264	152
252	110	9.341	8.5	.53- .77	43,014	391
268	147	5.308	3.6	.60- .80	13,747	94
275	146	11.860	8.2	.57- .83	38,959	286
287	176	12.972	7.4	.67- .83	24,877	141
305	221	22.710	10.3	.57- .80	110,017	498

The mean number of advanced eggs per gram of fish is 229 for sample J-45-13, 243 for sample J-45-27, and 192 for the *Cobb* 1963 samples. Owing to the great range of individual values in each of the samples, there is no significance in the differences between the means. The mean for the 50 fish in the three samples is 216 eggs per gram of fish. The standard error of the mean is 15 eggs or about 7%. In spite of some rather low fecundities, the distribution of eggs per gram of fish approximates a normal distribution indicating that these low counts are within the limits of expected variation.

Eggs/gram	*Percent frequency*
< 50	2
100	24
200	38
300	30
400	2
500	2
>550	2

The low counts apparently did not result from partial spawning of the advanced mode because they were found in fish that were not yet ripe.

RATIOS

To obtain estimates of the numbers of advanced eggs in the hake ovary, first about 100 yolked eggs in the sample were measured in order to delimit the distributions of advanced- and small-yolked eggs. Then the additional advanced-yolked eggs in the weighed sample were counted. An estimate of the numbers of small eggs was obtained from the ratio of large to small eggs in the measured frequency distribution, but because this estimate is based on relatively few eggs it is less accurate than the estimates of advanced eggs. Estimates of the numbers of small eggs per gram of fish ranged from

33 to 766 and averaged 248. This compares with 38 to 556 with an average of 216 for the advanced eggs for all samples.

The correlation obtained by MacGregor (1966) between percentage of eggs in the advanced mode and advanced eggs per gram of fish has no mathematical significance because both variables are related. Actually there is no relation between the number of advanced eggs and the number of small eggs. Ovaries containing either high or low numbers of advanced eggs per gram of fish may contain either high or low numbers of small-yolked eggs. However, the conclusion that the great variation in the ratios of large to small eggs makes multiple spawning unlikely seems to be valid.

Of 366,093 hake larvae taken on monthly cruises in the 6 years 1951 through 1956, 87% were taken in January, February, and March, 11.5% in April, and the remaining 1.5% in the remaining 8 months. Several large samples of hake taken off California in April 1970 showed that the advanced eggs were no longer present in the ovaries of the females while the smaller yolked eggs were. Because there is no evidence of further egg development in the ovaries and no evidence of heavy spawning subsequent to April in the plankton, we must assume that these small-yolked eggs are resorbed following spawning of the advanced mode.

SIZE AT FIRST MATURITY

One hundred thirty-six hake from sample J-45-13 (southern Baja California) were examined for stage of sexual maturity. Eighty hake from sample J-45-27 (central Baja California) and an additional seven hake taken in 1961 near Cedros Island (central Baja California) were also examined (Table 3).

In sample J-45-13 the largest immature male was 127 mm in length, and the largest immature female 138 mm. The smallest maturing male was 119 mm, and the smallest maturing female 125 mm. All males 129 mm and longer and all females 140 mm and longer were maturing.

In sample J-45-27 the range of fish length was not as good for determining size at first maturity. The smallest maturing male was 137 mm long, and it appeared that all males 159 mm and longer were mature. The smallest mature female was 222 mm in length, and all females of this length and longer were maturing. However, on the basis of the 1961 sample it appears that all females were maturing at some length between 202 and 222 mm.

It is difficult to determine the size at first maturity for hake off northern Baja California and California because very few fish of suitable size, taken during the spawning season, were available. For off-season hake the gonad index may

TABLE 3.—Size at first maturity. Southern Baja California, sample J-45-13, lat 27°07′ N, long 113°07′ W, January 11, 1970. Central Baja California (Cedros Island area), sample J-45-27, lat 28°44′ N, long 115°15′ W, January 16, 1970, and sample B-6111-3, Cedros Island, November 25, 1961. Males judged mature or immature by size and appearance of testes. Females judged immature if largest eggs in ovary were 0.20 mm or less in diameter (not yolked); probably maturing if maximum egg diameter was 0.23 to 0.47 mm; mature if maximum egg diameter was 0.50 mm or larger. Immature, not sexed: gonads not developed enough so that sex can be determined by gross examination.

Sample	Males			Females				Not sexed	
	Standard length	Immature	Mature	Standard length	Maximum egg diameter (*mm*)			Standard length	Immature
					0-0.10	0.30-0.47	0.50-0.77		
	mm			*mm*				*mm*	
J-45-13	119-127	6	6	122-124	6	0	0	100-118	19
				125-128	8	1	0		
	129-166	0	50	130-138	9	4	6		
				140-202	0	0	21		
					Maximum egg diameter (*mm*)				
					0-0.20	0.37	0.67-0.83		
J-45-27	137-140	1	1	172-197	3	0	0	120-138	42
	159-307	0	21	222-228	0	1	1		
				230-305	0	0	10		
B-6111-3				236	0	0	1	148-202	6

indicate maturity. Generally, hake with gonad indices of less than 0.5 (i.e., the gonad weight is less than 0.5% of the fish weight) do not contain yolked eggs in their ovaries. There is no yolk in eggs up to 0.20 mm diameter, and fish containing such eggs a few months before or after the spawning season may be considered immature. Eggs in an ovary having a gonad index of 0.8 have a maximum diameter of about 0.34 mm and at a gonad index of 1.5, about 0.43 mm maximum diameter. The eggs generally are not large enough to count (over 0.65 mm diameter for the largest eggs in the ovary) until the gonad index is about 3.5, and then only for fish having a fecundity of less than 100 eggs per gram of fish. If we apply the same criterion (a gonad index of less than 0.5 as indicating an immature fish) to the males, we can roughly estimate the size at maturity for off-season hake.

Applying this criterion of maturity to a number of miscellaneous hake samples taken in the off-season for spawning off northern Baja California and southern California, it appears that all males 285 mm and longer and all females 340 mm and longer were mature.

Best (1963) estimated that all hake, both males and females, taken off northern California were mature at 400 mm total length (about 360 mm standard length). The length at which all fish are mature could be somewhat less as he had a limited number of smaller fish in his samples.

Nelson and Larkins (1970) found that all fish of 450 mm total length (about 405 mm standard length) were mature in the Pacific Northwest. Apparently they also had few smaller fish to work with, and the length at which all fish are mature could be somewhat less.

DISCUSSION

The mean number of eggs per gram of fish was not significantly different among the three samples, J-45-13, J-45-27, and *Cobb* 1963. These three samples were taken in widely separated localities, and although they were similar with respect to relative fecundity, questions have been raised as to the distinctness of the north Pacific hake with respect to race or even species.

Ginsberg (1954) assigned the north Pacific hake to two species based on morphometric and meristic characters. His descriptions were based on 12 specimens of *Merluccius productus* taken off Washington, Oregon, and California, as far south as San Diego, and eight specimens of *M. angustimanus* taken in the Gulf of Panama, the Gulf of California, off the Pacific Coast of Baja California, and off Del Mar, Calif.

Ahlstrom and Counts (1955) could find no evidence of more than one species of hake in their extensive collections of eggs and larvae taken between San Francisco and the southern tip of Baja California. All of the small fish that had fully developed dorsal and anal fins had fin ray counts that fell within the range of *M. productus* but outside of the range of *M. angustimanus* as given by Ginsberg.

F. H. Berry (unpublished data) studied numerous additional specimens of hake from Baja California and California. He concluded that *M. productus* and *M. angustimanus* were the same species and the differences in meristic and morphometric characters, used by Ginsberg to separate the species represented a latitudinal cline.

There was certainly a marked cline in size at maturity for the hake used in this study, especially when these data are compared with data given by other authors. The size at which all fish were mature was as follows:

	Sex	*Standard length*
Southern Baja California	males	129 mm
	females	140 mm
Central Baja California	males	159 mm
	females	202-222 mm
Northern Baja California and southern California	males	285 mm
	females	340 mm
Northern California (Best, 1963)	both	360 mm
Pacific Northwest (Nelson and Larkins, 1970)	both	405 mm

The differences between areas are so great that the roughness of some of the estimates does not affect the conclusion that these differences are very real.

The distribution and growth patterns of the European hake, *M. merluccius,* is similar to that of *M. productus* in many ways. The European hake ranges from Norway to at least Mauritania in Africa (Hart, 1948) while *M. productus* ranges from Alaska to at least the southern tip of Baja California. Both species grow to much larger sizes in the northern parts of their ranges, but are much smaller in their southern ranges. *M. merluccius* in the Mediterranean Sea is smaller than the north Atlantic form, and both the southern Baja California and African coasts apparently produce dwarf races of their respective hake species.

Most recent information from the Guinean Trawling Survey (Williams, 1968) shows that there are continuous populations of hake from Norway to South Africa. However, the hake taken off the west coast of Africa are ascribed to several species other than *M. merluccius*. The West African hake, *M. polli* and unidentified *M.* spp. were taken throughout the survey area from the Gambia border to the Congo. The Senegal hake *M. senegalensis* was taken in the northern areas between the Gambia border and southern Liberia with one questionable record from Nigeria, and the South African hake *M. capensis* was taken in the southern areas between Cameroun and the Congo. A sample of 50 *M. senegalensis* averaged 26.3 cm total length (range 18 to 27), and a sample of *M. polli* averaged 41.7 cm total length (range 35 to 49).

SUMMARY

The north Pacific hake, *Merluccius productus*, ranges from Alaska to at least southern Baja California.

The fecundity of individual hake varied greatly off Baja California and southern California, but there was no significant difference in average fecundity among the samples taken from widely separated sampling stations in this area. Estimates of the number of advanced eggs contained in 50 prespawning hake averaged 216 eggs per gram of fish.

Average size at first maturity for female hake varied from 133 mm standard length off southern Baja California to about 340 mm off northern Baja California and southern California. Males appeared to mature at smaller sizes 128 mm in the south to 285 mm in the north.

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7133

COLOR PATTERNS OF PILOTFISH (*NAUCRATES DUCTOR*) AND THEIR POSSIBLE SIGNIFICANCE.—Two color patterns and the behavior of pilotfish (*Naucrates ductor*) were observed near the equator in the central Pacific from underwater windows of a drifting raft (Gooding, 1965; Gooding and Magnuson, 1967). Pilotfish, associated with whitetip sharks (*Carcharhinus longimanus*), were observed from 11 to 13 March 1964. From one to seven pilotfish 8–20 cm long and from one to four remora (*Remora remora*) were associated with each shark.

Typical coloration of pilotfish includes about eight black vertical bars (including those on the head and the caudal fin) against a light silvery background (Fig. 1). Further description and a good figure are presented by Marshall (1965).

A transient coloration of pilotfish, previously unreported in the literature, was also observed from the raft. The characteristic black vertical bars faded and disappeared, leaving the fish with a silvery-white appearance with some bluish color on the dorsum. This bluish color, when observed closely, consisted of about three broad patches in tandem across the dorsum (Fig. 2). Borders between the bluish and whitish areas were not sharply defined. The lower half of the fish's body remained whitish.

This transient coloration was recorded during 16 observations of sharks and their associated pilotfish. It occurred only when the pilotfish from more than one shark intermingled. One pilotfish while chasing another lost its bars and exhibited the transient coloration during the chase. The more intense the chase, the more dramatic the color change seemed to be. When chasing activities stopped, the typical barred coloration returned. This sequence was observed many times. Usually the pursuing fish was larger than the pilot fish being chased. If the smaller fish were chased the chased fish did not lose its barred coloration. If two fish were similar in length, the bluish-white coloration appeared in both fish, but less intensely in the chased fish. The smaller fish was sometimes driven as far as 5 m from its shark. Several times a pilotfish also chased a remora. Transient coloration did not appear when the pilotfish ate pieces of fish we tossed into the water nor when they chased natural foods.

These interactions occurred between pilotfish from the same shark or from different sharks. They did not occur, however, when only one shark was present, even though a number of pilotfish accompanied the shark. Nor did they always occur when several sharks were present. Pilotfish always separated and stopped chasing each other when two sharks swam away from each other. Usually the pilotfish remained with their original shark, but since the pilotfish could not be identified with certainty some permanent interchange of fish could have taken place. Identification of pilotfish was based largely on size.

Transient coloration appeared to be part of an aggressive threat display in defense of the shark as a moving territory. The expectation would be that these interactions would drive the smaller pilotfish from a shark, thus reducing intraspecific competi-

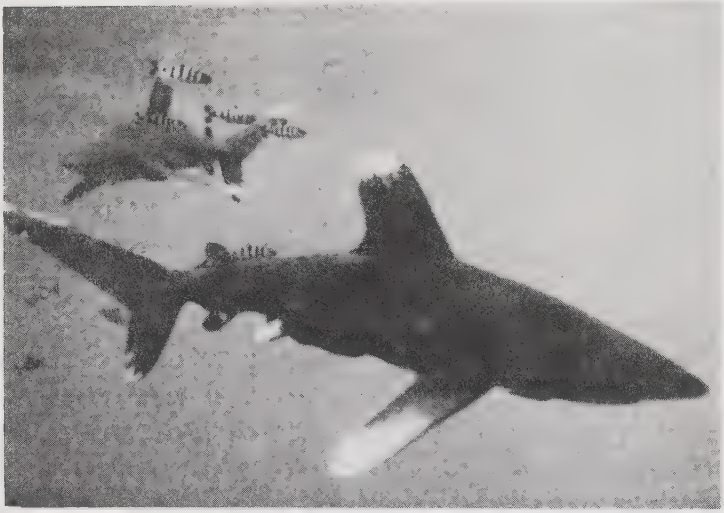

Fig. 1. Whitetip sharks (*Carcharhinus longimanus*) with pilotfish (*Naucrates ductor*) photographed from a drifting raft in the central Pacific Ocean.

tion for the larger dominant pilotfish. Aggression should be more successful in driving off the smaller fish if an alternative shark were available for the subordinates. Ineffectiveness of aggression in the absence of an alternative residence might explain the absence of aggression when only one shark was present.

Since pilotfish apparently defend the shark as a moving territory, they would be expected to obtain some benefit from the association. The most significant benefit may be protection from predation. Once, pilotfish pursued by a dolphin (*Coryphaena hippurus*) were observed to flee to the raft and then to the shark. For the following 30 min their attraction to the shark appeared greater than usual. Protection from predation was the most obvious benefit that a variety of fishes obtained by associating with a drifting raft (Gooding and Magnuson, 1967). Fishes at the raft often avoided predators by swimming close under the raft when predators approached. Once a golden jack (*Caranx kalla*) left the raft in the company of a shark without being attacked by dolphins which had previously chased the jack to the raft.

Other potential advantages of an association with sharks are 1) the shark is used as a substrate for depositing eggs, 2) pilotfish feed on the ectoparasites of the shark, and 3) pilotfish depend on the fragments of the fish being eaten by the shark or the feces of the shark. But Whitley (1951) pointed out that data to support these ideas are largely nonexistent or even contradictory. Pilotfish in the boundary layer around a swimming shark should also obtain an advantage of traveling with little expenditure of energy (Shuleikin, 1958). We did not observe pilotfish spawning, nor eating the numerous ectoparasites present on the sharks. When food was tossed to the sharks, pilotfish ate fragments broken by the feeding of the shark. Yet pilotfish did not depend upon fragments as they also foraged independently on small fishes and zooplankton. One pilotfish swam for 3 min on its side immediately adjacent to the upper surface of the shark's pectoral

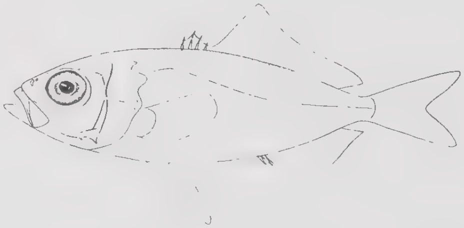

Fig. 2. A diagrammatic sketch of the transient coloration of pilotfish.

fin, with little caudal movement evident. These aspects of the association would appear less important than predator avoidance.

The barred coloration may be important to predator avoidance because it has some features of an aposematic display. Cott (1957) summarized features of an aposematic display—the pattern of coloration is usually bold and consists of vivid tones such as black, white, or shades of red. The animal is highly conspicuous in nature. Some feature of an aposematic animal or its immediate environment is potentially dangerous or noxious to a predator—for example, the smell of a skunk. The pilotfish has the conspicuous coloration. They were readily visible to us and could be identified as pilotfish near the maximum range of visibility. The shark provides the potential danger. Pilotfish, observed from the raft, were not always adjacent to the shark as usually pictured, but wandered out to the limits of visibility, apparently on feeding forays. When a predator encounters the conspicuous markings of the pilotfish in the monotonous epipelagic environment, the stimulus could signal the presence of a shark nearby and thus reduce the likelihood that feeding behavior would be released in the predator.

Some other fishes that associate with animals potentially dangerous to predators are also conspicuously marked and may be aposematic animals. Amphiprionids or anemone fishes have vivid white and orange or white and brown vertical bands and live in close association with anemones. Juvenile omaka (*Caranx mate*) have dark vertical bars and live in association with jellyfish (Gosline and Brock, 1960). A number of other examples can be found among fishes.

These observations suggest that the transient coloration of pilotfish is part of an agonistic display and that the typical coloration of pilotfish may be aposematic. A more definite conclusion, especially in regard to the typical coloration, will have to await additional and more critical observations.

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7134

GILL RAKER APPARATUS AND FOOD SELECTIVITY AMONG MACKERELS, TUNAS, AND DOLPHINS

John J. Magnuson and Jean G. Heitz[1]

ABSTRACT

Gill raker morphology and fork length were measured from 411 fish, representing eight species of scombrids and two species of coryphaenids (dolphin). For each species linear regressions passing through the origin were determined relating mean gill raker gap in millimeters (first gill arch) with fork length in centimeters (l), and log filtering area (first gill arch) with log fork length. Mean gill raker gaps equaled: *Auxis rochei*—$0.0144l$, *Katsuwonus pelamis*—$0.0211l$, *Auxis thazard*—$0.0213l$, *Thunnus albacares*—$0.0344l$, *Thunnus alalunga*—$0.0365l$, *Euthynnus affinis*—$0.0386l$, *Thunnus obesus*—$0.0391l$, *Sarda chiliensis*—$0.0509l$, *Coryphaena hippurus*—$0.0650l$, *Coryphaena equisetis*—$0.0655l$, and *Acanthocybium solanderi*—no gill rakers. Among the species gill raker gap was directly proportional to the number of gill rakers, but no relation occurred between mean gap and filtering areas. Gill raker gap differed markedly among species and lengths of fish. A 50-cm *K. pelamis*, a 30-cm *T. albacares*, and a 10-cm *Sarda orientalis* all had an estimated mean gap of 1 mm. Conversely the gaps of a 50-cm fish of each species were estimated to be ca. 1.0, 1.7, and 4.5 mm respectively.

Mean gill raker gaps from this study were compared with the percentage of crustaceans in stomachs of Central Pacific fishes based on literature records. Body sizes of fishes and squids in the stomachs were larger than crustaceans. Percent volumes that crustaceans contributed to the stomach content were inversely related to mean gaps (Kendall rank correlation coefficient, $\tau = -0.59$, $n = 16$, $P < 0.001$). Partial correlation indicated that gap was more important than fork length in predicting the quantity of crustaceans. Thus, the gill raker gap was related functionally with the quantity of smaller organisms in the stomachs. Presence of euphausids in stomachs of *K. pelamis* and their absence in *T. albacares* from the eastern tropical Pacific may result from the small size of euphausids and the smaller gill raker gaps of *K. pelamis* relative to *T. albacares*. Gill raker gap and the maximum distensibility of the esophagus would set physical limits on the size of food eaten. The diverse fauna assemblage of crustaceans, fishes, and squids within this size range has masked to a great extent the selective feeding that does occur among scombrids and coryphaenids on the basis of food size.

Most scombrid fishes have a varied diet that includes numerous crustaceans, cephalopod molluscs, and fishes. The Indian mackerel, *Rastrelliger kanagurta* (Cuvier), even eat phytoplankton (Bhimachar and George, 1952). The high diversity of organisms in their stomach contents has generated the opinion that scombrids are nonselective feeders, preying upon anything they encounter. Coryphaenid fishes, dolphins, eat fish predominantly.

Yet selectivity does exist in food habits of scombrids. Within a species, larger fish contain relatively fewer crustaceans and more fishes. Crustaceans constituted 44% of the stomach volume of skipjack tuna, *Katsuwonus pelamis* (Linnaeus), shorter than 50-cm fork length but only 1.5% of the volume for fish longer than 60 cm (Yuen, 1959). Similarly, crustaceans constituted 35% of the stomach volume of yellowfin tuna, *Thunnus albacares* (Bonnaterre), shorter than 130 cm but only 1% for those longer than 130 cm (Reintjes and King, 1953). Reintjes and King suggested that these differences might result, as the fish grew, from a change in food preference or a change in the ability to search out and capture larger, more mobile prey (fishes). Another consideration, in our view, is that larger predators have a reduced ability to catch small prey (crustaceans).

Prevention of food loss through the opercular gap is generally recognized as the primary function of gill rakers. Species with more closely

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spaced gill rakers are more likely to feed on plankton than those with more widely spaced rakers (Suyehiro, 1942; Yasuda, 1960a; Brooks and Dodson, 1965; Kliewer, 1970).

This paper (1) quantitatively describes the gill raker apparatus of certain scombrids and coryphaenids with respect to the gap between gill rakers and the filtering area of the first gill arch, (2) compares differences in gill raker gap among species and lengths of fish, and (3) considers the proposition that observed inter- and intraspecific variations in the diet are associated functionally with the morphometrics of the gill raker apparatus.

MORPHOMETRY OF GILL RAKER APPARATUS

Gill raker morphometry and fork length were measured from 411 fish, representing eight species of scombrids and two species of coryphaenids. Albacore, *Thunnus alalunga* (Bonnaterre), were from the commercial longline fishery operated from American Samoa, the Pacific bonito, *Sarda chiliensis* (Cuvier), were from waters off Palos Verdes, Calif., and chub mackerel, *Scomber japonicus* Houttuyn, were from the Honolulu fish market. All other specimens were from Hawaiian waters and were caught with pole and line or longline by commercial fishermen or on numerous cruises of the research vessel *Charles H. Gilbert* of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu (now National Marine Fisheries Service Hawaii Area Fishery Research Center).

Measurements were from the first right gill arch of fresh or thawed specimens. The arch was removed from the fish and extended by pulling the upper and lower branches apart until the rakers were stiffly erect. Gaps between adjacent rakers (Figure 1) were measured at the base of the rakers by expanding a vernier caliper until the two gill rakers began to spread apart. Arch length and gill raker length were also measured with the caliper (Figure 1). Depending on the species, six to nine gaps and six to eight gill raker lengths spaced along the arch were obtained from scombrids and three gaps and five gill raker lengths from coryphaenids. Mean gap was the average of those measured along the arch. A gap near the middle of the lower arch was also used to represent gap width in the primary filtering area. Filtering area was calculated from average length of gill rakers and length of the arch. Lower and upper arch filtering areas were computed separately and summed.

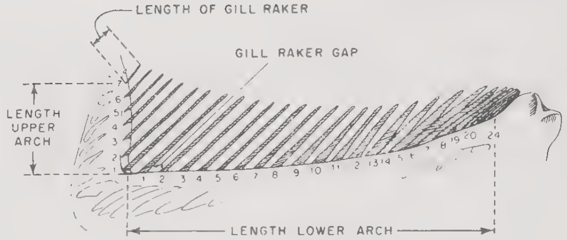

FIGURE 1.—Diagram of the first right gill arch of a scombrid as viewed from oral chamber showing the morphometric measurements. Numbers indicate particular rakers.

DESCRIPTION

Gill rakers of the first arch of most scombrids were conspicuous and well developed. Inner edges of the rakers of most species were covered with numerous short, spiny protuberances. For *S. japonicus*, these spines were thin, about as long as the gill raker gap, and evenly spaced to form a finer sieve between adjacent gill rakers. The other three arches of scombrids lacked gill rakers, but smaller rakerlike processes on the inner faces of the all arches projected posteriorly to the adjacent arch forming a sieve. Inner edges of these processes had short, spiny protuberances similar to the gill rakers.

Rakers were articulated so that they became stiffly erect forming a parallel row of blade-shaped rakers when the acute angle between the upper and lower arch was expanded toward 90 degrees. In the branchial chamber the tips of the rakers extended to the inner surface of the flared gill cover.

The wahoo, *Acanthocybium solanderi* (Cuvier), has no gill rakers, but most scombrids have more than 20 elongated rakers—*K. pelamis* in our samples had 53 to 64. Longest rakers were near the joint between the upper and lower branches of the arch. They became progressively shorter toward the ends of the arch. For example, a *K. pelamis* 50 cm long had gill rakers 21 mm long at the joint but only 2 and 8 mm at the ends of the upper and lower branches, respectively. The largest gap (1.8 mm) was near the center of the lower branch. Gaps were smaller on the upper branch than lower branch and were most narrow at the ends of the arch (0.2 mm and 0.9 mm for the upper and lower branches). Often the gap between the first raker of the upper and the first raker of lower arch was as great as the widest gap on the lower arch.

Most of the filtering area of scombrids was confined to the lower branch of the gill arch. The lower branch comprised 73 to 80% of the total. The filtering area of coryphaenids was essentially restricted to the lower arch. Dolphin, *Coryphaena hippurus* Linnaeus, had no rakers on the upper arch, pompano dolphin, *Coryphaena equisetis* Linnaeus, had only one.

Gill rakers of the two coryphaenids were shorter and more uniform in length than those of scombrids. The longest gill raker from a 55-cm *C. equisetis* was only 9 mm contrasted

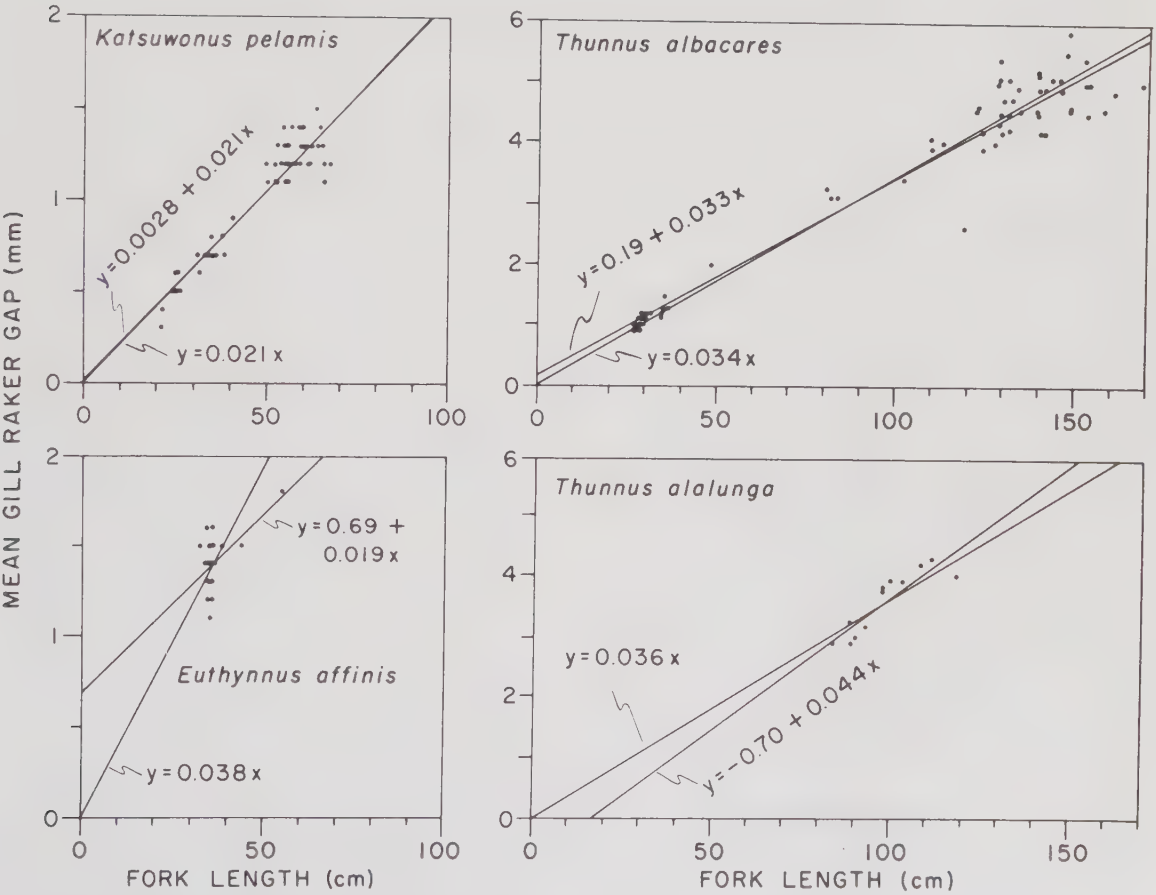

FIGURE 2.—Relation between mean gill raker gap and fork length showing the advantage of using regression through the origin for predicting mean gill raker gap especially when sample sizes are small and restricted in length range.

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to 21 mm from a 50-cm *K. pelamis*. Even the longest raker of a 125-cm *C. hippurus* was only 16 mm—shorter than that of a 50-cm *K. pelamis*.

SIZE AND SPECIES COMPARISONS

METHODS

Linear regressions relating gill raker gap to fork length and log filtering area to log fork length were computed for each species. Regressions were computed once about the mean, and a second time, were forced to pass through the origin. The latter procedure was used because the ranges of fork lengths of some species were not sufficient to obtain reasonable equations (Figure 2).

Both *K. pelamis* and *T. albacares* were represented by large samples that included small and large specimens. Their regressions of gill raker gap on fork length passed close to the origin even when not forced to do so; the y-intercept was 0.00 mm for *K. pelamis* and 0.19 mm for *T. albacares* (Figure 2). In contrast, kawakawa, *Euthynnus affinis* (Cantor), and *T. alalunga* were represented by small samples that did not include small specimens. Regressions of gill raker gap on fork length for these two species did not closely approach the origin (Figure 2); we believe these equations would also have had y-intercepts near 0.0 mm if lengths of our specimens had been more evenly distributed. Since some comparisons were made that extrapolate outside the size ranges represented in our samples, the regressions forced to pass through the origin were used for all computations of gill raker gap.

The same reasoning was used for the relations between log filtering area and log fork length. In this case, the zero-zero intercept was equivalent to 1 cm fork length and 1 mm^2 filtering area rather than zero fork length and zero filtering area. Since most comparisons made later were for fish at least 35 cm long with filtering areas near 100 mm^2, errors owing to the position of the intercept were believed negligible.

SIZE AND SPECIES COMPARISONS

Linear regressions passing through the origin that relate gill raker gap to fork length and log filtering area to log fork length are presented in Table 1 along with the numbers and lengths of fishes measured.

Mean gill raker gap increased with fork length and was equal to 1.4 and 6.6% of fork length for frigate mackerel, *Auxis rochei* (Risso), and *C. hippurus*, respectively. Gill raker gap in the middle of the lower branch was usually 1.0 to 1.2 times the mean gill raker gap except for *A. rochei* (1.3) and *K. pelamis* (1.4). Mean gap increased in direct proportion to fish length; i.e., if length doubled, gap also doubled.

TABLE 1.—Linear regressions passing through the origin that relate mean gill raker gap to fork length and log filtering area to log fork length and the number and length of fish measured.

Species	Number of fish measured	Regressions of gap (G) and fork length (l)	Fork length		G (mm)	Standard error of estimate for G (mm)	Regressions of log filtering area (log A) and log fork length (log l)	Mean		Standard error of estimate for Log A (mm^2)
			Mean (cm)	Range (cm)				Log l (cm)	Log A (mm^2)	
Sarda chiliensis	8	$G = 0.0509\ l$	50.13	38.7- 58.8	2.56	0.27	log A = 1.73 (log l)	1.7001	2.9246	0.0584
Auxis thazard	16	$G = 0.0213\ l$	31.40	25.1- 35.7	0.67	0.10	log A = 1.79 (log l)	1.4969	2.6730	0.0393
Auxis rochei	11	$G = 0.0144\ l$	30.24	29.2- 32.9	0.44	0.06	log A = 1.78 (log l)	1.4706	2.6291	0.0192
Euthynnus affinis	25	$G = 0.0386\ l$	36.29	33.4- 54.6	1.41	0.29	log A = 1.82 (log l)	1.5598	2.8421	0.0234
Katsuwonus pelamis	63	$G = 0.0211\ l$	47.60	21.0- 67.5	1.00	0.10	log A = 1.83 (log l)	1.6776	3.0135	0.0697
Thunnus alalunga	12	$G = 0.0365\ l$	98.56	84.0-118.8	3.59	0.25	log A = 1.81 (log l)	1.9937	3.6088	0.0343
Thunnus albacares	74	$G = 0.0344\ l$	94.86	27.1-166.9	3.31	0.36	log A = 1.78 (log l)	1.9771	3.3468	0.0405
Thunnus obesus	82	$G = 0.0391\ l$	132.96	75.2-175.3	5.26	0.60	log A = 1.85 (log l)	2.1236	3.9058	0.0449
Coryphaena equisetis	38	$G = 0.0655\ l$	94.90	30.8- 58.7	6.16	0.54	log A = 1.39 (log l)	1.9773	2.7339	0.0704
Coryphaena hippurus	68	$G = 0.0650\ l$	40.52	63.2-126.4	2.69	0.34	log A = 1.36 (log l)	1.6077	2.1716	0.0727

Filtering area increased as the 1.4 to 1.8 power of fork length. When these regressions were not forced to pass through the origin, the filtering area increased as the 2.2 power of fork length for *K. pelamis* and the 1.9 power for *T. albacares.* Forcing the regressions to pass through the origin may have decreased the slope.

To facilitate comparison of different species, the mean gap and filtering area were computed from the regression in Table 1 for fish with a fork length of 35 cm. These are listed in Table 2 in order of decreasing number of gill rakers, increasing gap, and decreasing filtering area.

As expected, the number of rakers and gill raker gap were closely related (Table 2). Lack of complete correspondence may have resulted from differences in the thickness of gill rakers, differences in the length of the gill arch, or both.

Among scombrids no relation was evident between filtering area and number of rakers or between filtering area and mean gill raker gap (Table 2). Apparently, the length of raker was an important variable determining differences in filtering area among species. Coryphaenids had a larger gill raker gap and smaller filtering area than any scombrid except striped bonito, *Sarda orientalis* (Temminck and Schlegel).

TABLE 2.—Scombrid and coryphaenid species (35-cm fork length) listed in order of increasing numbers of gill rakers, and decreasing mean gill raker gap and filtering area. (Data on *S. orientalis* from one fish, *S. japonicus* from two fish.)

Rank	Mean number of rakers (n)	Species	Mean gill raker gap (mm)	Species	Filtering area (mm^2)	Species
12	8	*Coryphaena hippurus*	3.3	*Sarda orientalis*	--	*Scomber japonicus*
11	10	*Coryphaena equisetis*	2.3+	*Coryphaena equisetis*	685	*Thunnus obesus*
10	11	*Sarda orientalis*	2.3—	*Coryphaena hippurus*	650	*Euthynnus affinis*
9	25	*Sarda chiliensis*	1.8	*Sarda chiliensis*	620	*Thunnus alalunga*
8	26	*Thunnus obesus*	1.4	*Thunnus obesus*	530	*Katsuwonus pelamis*
7	29	*Thunnus alalunga*	1.4	*Euthynnus affinis*	570	*Auxis thazard*
6	30	*Thunnus albacares*	--	*Scomber japonicus*	550	*Auxis rochei*
5	31	*Euthynnus affinis*	1.3	*Thunnus alalunga*	450	*Sarda chiliensis*
4	37	*Scomber japonicus*	1.8	*Thunnus albacares*	410	*Thunnus albacares*
3	40	*Auxis thazard*	0.74	*Auxis thazard*	--	*Sarda orientalis*
2	45	*Auxis rochei*	0.74	*Katsuwonus pelamis*	135	*Coryphaena hippurus*
1	58	*Katsuwonus pelamis*	0.51	*Auxis rochei*	120	*Coryphaena equisetis*

Among scombrids 35 cm long, *Sarda* had the largest gaps (1.8-3.3 mm) and *Auxis* and *Katsuwonus* the smallest (0.51-0.74 mm). *Thunnus, Euthynnus,* and *Scomber* had intermediate gap widths (1.2-1.4 mm). Among *Sarda, Auxis,* and *Thunnus* represented in our samples, species within genera had more similar gill raker gaps than those in different genera. On this basis alone food habits for fish of the same length would be expected to be more similar within genera than among genera.

Mean gill raker gap differed markedly with species and length of fish (Figure 3). For example, a 50-cm *K. pelamis,* a 30-cm *T. albacares,* and a 10-cm *S. orientalis* all had a mean gill raker gap of approximately 1 mm. Conversely, gill raker gaps of these three species differed markedly at the same fork length. Gaps of 50-cm *K. pelamis, T. albacares,* and *S. orientalis* were ca.

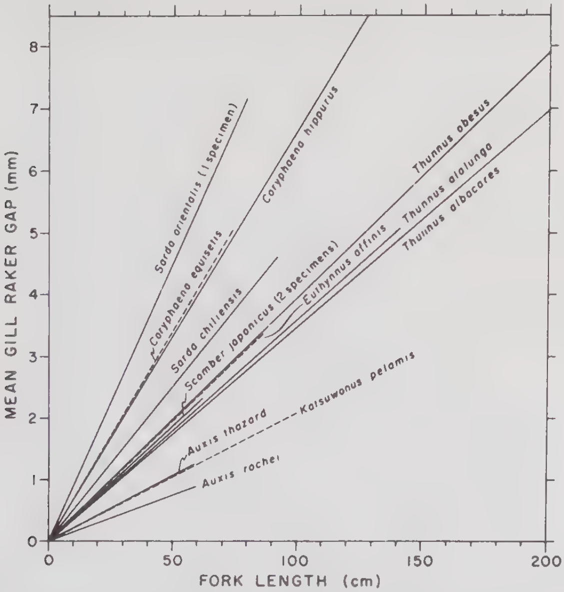

FIGURE 3.—Comparison of the mean gill raker gap and fork length relationship for various scombrid and coryphaenid fishes. Lengths shown approximate ranges known for each species.

TABLE 3.—The average size of individual crustaceans, squids, and fishes in the stomachs of scombrids from the central Pacific.

Species	Volume of individual organisms (ml)			Volume of food analyzed (*ml*)	Source
	Crustaceans	Squids	Fishes		
Thunnus albacares	0.3	4.8	6.4	44,680	King & Ikehara (1956)
Thunnus obesus	0.6	9.5	8.2	22,297	King & Ikehara (1956)
Thunnus albacares	0.2	3.8	4.6	52,336	Reintjes & King (1953)
Katsuwonus pelamis	0.2	4.3	3.7	13,974	Waldron & King (1963)
Mean (unweighted)	0.3	5.6	5.7		

1.0, 1.7, and 4.5 mm, respectively. Selectivity of the gill raker apparatus would vary with gill raker gap, a function of both species and length of the fish. Thus, a small *T. albacares* and a large *K. pelamis* should have more similar diets than a small and a large *T. albacares.* Any number of such predictions can be generated from Figure 3. A fish with smaller mean gap, regardless of its species or length, would be expected to be more planktivorous.

RELATION BETWEEN GILL RAKER GAP AND DIET

Stomach-content data from published literature from the central Pacific were compared with the mean gill raker gaps reported here to test the hypothesis that fish with a finer gill raker gap have a greater proportion of smaller organisms (crustaceans) in their diet.

Crustaceans in the diet of scombrids from the central Pacific were smaller than were the other major food organisms (squids and fishes) (Table 3). The volume of individual, partially digested crustaceans in the stomachs of five species averaged 0.3 ml whereas individual, partially digested squids and fishes averaged 5.6 and 5.7 ml, respectively. The much smaller body size of the crustaceans was not likely the result of differential digestion, especially since the exoskeleton of crustaceans, if anything, might be expected to slow, rather than accelerate, digestion (Pandian, 1967).

For comparison with gill raker data, the percent volumes of the stomach content comprised by crustaceans, squids, or fishes are presented in Table 4 for five scombrids and one coryphaenid. Only stomach data from the central Pacific were used because differences in typical body size of crustaceans in scombrid stomachs from other regions would have invalidated these

TABLE 4.—Food of scombrid and coryphaenid fishes from the central Pacific divided into the percentages of the stomach volume that were crustaceans, squids, or fishes. The median fork length of fishes in the sample is also given along with the literature source for the data.

Species	Stomach content (*percent* volume)			Fork length		Number of stomachs	Literature source
	Crustaceans	Squids	Fishes	Median (*cm*)	Range (*cm*)		
Acanthocybium solanderi	0	0	100	111	104-123	3	Tester & Nakamura (1957)
Acanthocybium solanderi	0	--	--	--	54-198	235	Iversen & Yoshida (1957)
Euthynnus affinis	8	0	92	49	31-67	32	Tester & Nakamura (1957)
Katsuwonus pelamis	44	--	40	44	39-49	>25	Yuen (1959)
Katsuwonus pelamis	4.0	23	72	47	33-60	305	Waldron & King (1963)
Katsuwonus pelamis	67	7	26	50	40-61	67	Tester & Nakamura (1957)
Katsuwonus pelamis	25	--	70	55	50-60	>25	Yuen (1959)
Katsuwonus pelamis	3.7	19	74	73	60-89	254	Waldron & King (1963)
Katsuwonus pelamis	1.5	--	91	73	62-84	>25	Yuen (1959)
Thunnus albacares	45	14	33	80	53-100	544	Reintjes & King (1953)
Thunnus albacares	39	9	49	115	100-130	205	Reintjes & King (1953)
Thunnus albacares	1.7	29	65	135	85-140	188	King & Ikehara (1956)
Thunnus albacares	3	4	93	140	130-168	26	Reintjes & King (1953)
Thunnus albacares	0.8	30	60	148	140-175	251	King & Ikehara (1956)
Thunnus obesus	2.3	26	70	128	75-140	63	King & Ikehara (1956)
Thunnus obesus	1.4	36	58	158	140-200	103	King & Ikehara (1956)
Coryphaena hippurus	1.6	2	97	81	42-121	52	Tester & Nakamura (1957)

TABLE 5.—Percent crustaceans by volume in the stomachs, median fork length, mean gill raker gap, and species of fish. (Ranks are from smallest to largest and ordered by the percentage of crustaceans in the stomachs.)

Species	Crustacea		Median fork length		Mean gill raker gap	
	%	Rank	*(cm)*	Rank	*(mm)*	Rank
Acanthocybium solanderi	0	1	111	10	0	16
Thunnus albacares	0.8	2	148	15	5.2	13
Thunnus obesus	1.4	3	158	16	6.3	15
Katsuwonus pelamis	1.5	4	73	6	1.5	5
Coryphaena hippurus	1.6	5	81	9	5.3	14
Thunnus albacares	1.7	6	135	13	4.7	10
Thunnus obesus	2.3	7	128	12	5.1	12
Thunnus albacares	3	8	140	14	4.9	11
Katsuwonus pelamis	3.7	9	73	6	1.5	5
Katsuwonus pelamis	4.0	10	47	2	0.99	2
Euthynnus affinis	8	11	49	3	1.9	7
Katsuwonus pelamis	25	12	55	5	1.2	4
Thunnus albacares	39	13	115	11	4.0	9
Thunnus albacares	44	14	80	8	2.8	8
Katsuwonus pelamis	45	15	44	1	0.92	1
Katsuwonus pelamis	67	16	50+	4	1.0	3

analyses. The galatheids and portunids dominating the crustaceans found in *T. albacares* stomachs in the eastern tropical Pacific (Alverson, 1963) are much larger (Longhurst, 1967; Jerde, 1967b) than the typical crustaceans from the stomachs of central Pacific scombrids given in Table 3. Also, data were not used if fewer than 25 stomachs had been examined. None of the 238 *A. solanderi* contained crustaceans and 0% crustaceans in the stomach was considered a reasonable estimate for any larger *A. solanderi*. The median or midrange fork length of fish was determined for each set of stomach data. Then mean gill raker gaps for fish of those species and length were estimated with the regressions from Table 1. Data on median fork length, mean gill raker gap, and percent crustaceans by volume in the stomach are presented in numerical and ranked form in Table 5.

Percent volumes that crustaceans contributed to the stomach content were inversely related to mean gill raker gap (Figure 4a) (Kendall rank correlation coefficient, $\tau = -0.59$; $n = 16$; $P < 0.001$) and to fork length (Figure 4b) (Kendall rank correlation coefficient, $\tau = -0.45$; $n = 16$; $P < 0.01$). Several notable exceptions occurred in the relation with fork length (Table 5, Figure 4b). *C. hippurus*, 81 cm long, contained 2% crustaceans while *T. albacares*, 80 cm long, contained 45% crustaceans. *T. albacares*, 135 cm long, also contained 2% crustaceans. Not unexpectedly, *C. hippurus*, 81 cm long, and *T. albacares*, 135 cm long, both had mean gill raker gaps near 5 mm whereas the 81-cm *T. albacares* had a smaller mean gill raker gap near 3 mm. The somewhat closer correspondence of percentage of crustaceans to gill raker gap than to fork length can be observed by comparing Figures 4a and 4b or by comparing the associated probabilities of no correlation ($<.01$ versus $<.001$).

Kendall partial rank correlation coefficients were computed to determine the association between percent crustaceans in the stomach and gill raker gap, with the effect of fork length held constant. The partial correlation coefficient between percent crustaceans and gap, independent of variation in fork length, was —0.43 while the partial correlation between percent crustaceans and fork length independent of variations in gap, was only —0.05. Thus, although fork length was correlated with the percent crustaceans, this correlation resulted from the association between gill raker gap and fork length. Gill raker gap was the important variable correlated to percent crustaceans in the diet.

Data on percent crustaceans in the stomach by volume were also presented for *K. pelamis* and *T. albacares* of various size by Alverson (1963) and for *K. pelamis* and blackfin tuna, *Thunnus atlanticus* (Lesson), by Suarez Caabro

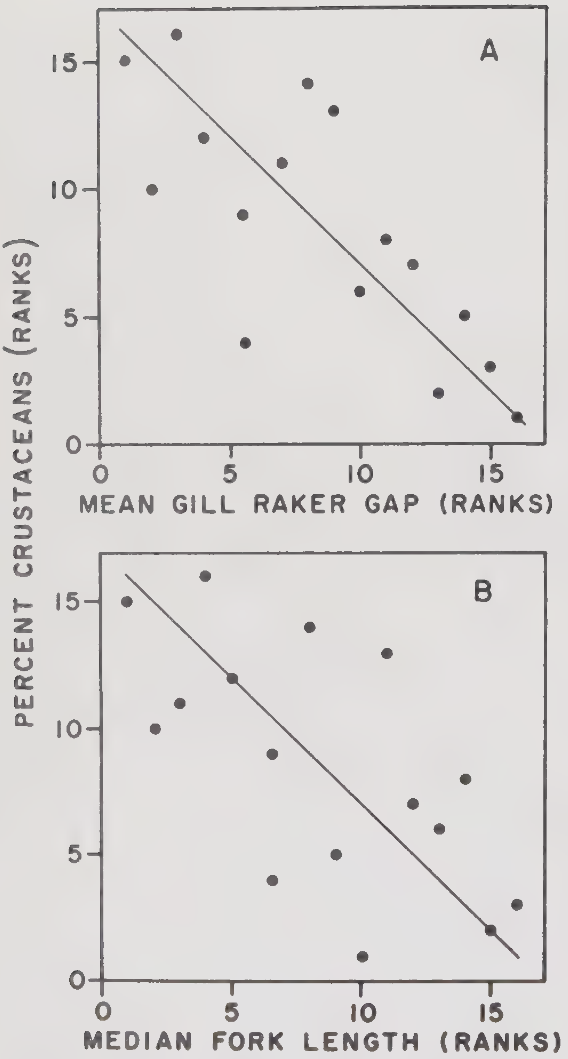

FIGURE 4.—Relation between percentage crustaceans by volume of diet (ranked) and the (a) mean gill raker gap of a fish (ranked) and (b) fork length of fish (ranked). The diagonal line depicts a perfect inverse relationship.

and Duarte Bello (1961). These were not used in the present analysis because sample sizes were fewer than 25 fish or because the size of the individual crustaceans was unavailable. Regardless, larger *K. pelamis* in both studies contained less crustaceans. However, larger *T. albacares* in Alverson's study tended to eat more crustaceans than did smaller specimens. This may have been because the crustaceans in their diet were relatively large.

Alverson's paper also presents a good example of selectivity among crustaceans that may be based on size of gill raker gaps. *K. pelamis* and *T. albacares* from the same areas had markedly different diets. Crustaceans contributing the greatest volume to the stomachs were galatheids and portunids for *T. albacares* but euphausids for *K. pelamis.* Euphausids were rare in stomachs of *T. albacares* even when common in the micronekton (Blackburn, 1968). Galatheids and portunids (Longhurst, 1967; Jerde, 1967b) are typically larger in size than euphausids (Jerde, 1967a). The small euphausids were not important in stomachs of *T. albacares* (i.e., 1% of the volume) in any of the areas of the eastern tropical Pacific studied by Alverson (1963), but the larger galatheids and portunids were important in the stomachs of *K. pelamis* from certain areas. The above observations would be the predictions from gill raker gaps—*T. albacares* have broader gaps than *K. pelamis* and would not be expected to capture the smaller crustaceans.

The major hypothesis under investigation in the present study was that the quantity of smaller organisms (crustaceans) eaten should be related to the selectivity of the gill raker apparatus. The above correlations on central Pacific data, although only crude in nature, lend support to this idea. A more definitive test would require extensive data on the size of food organisms and the diet of scombrids over more narrow length ranges than are available from the published literature.

Even though the structure of the gill raker apparatus ultimately determines the smallest size of prey, it is possible that actual selection of fishes is made prior to ingestion (Ivlev, 1961; Galbraith, 1967). Galbraith believed that the gill rakers of yellow perch, *Perca flavescens* (Mitchill), and rainbow trout, *Salmo gairdneri* Richardson, could have retained smaller zooplankton than were typically found in their stomachs. These species ate only larger *Daphnia* even though numerous smaller ones were in the zooplankton.

Several authors have pointed out that fish tend to select the largest food organisms available to them (Hayashi, 1956, as cited in Yasuda, 1960b; Ivlev, 1961; Brooks, 1968). The large mouth of larval scombrids facilitates capture of large copepods at first feeding and contributes to their rapid early growth rates (Shirota, 1970). The responsiveness of at least one scombrid to food is influenced by the size of the food organism—*K. pelamis* ate whole shrimp and squid at the beginning of a feeding, but as they became sated, they would only eat cut-up pieces of smaller size (Nakamura, 1962). Feeding behavior of Atlantic mackerel, *Scomber scombrus* Linnaeus, (Sette, 1950) and northern anchovy, *Engraulis mordax* Girard, (Leong and O'Connell, 1969) changes with the size of food. When small food is present, they open the mouth wide and flare the opercles in a filter feeding mode, but with larger food they make individual biting attacks. *S. japonicus* eats food smaller than would be predicted by gill raker gap (Hiyama and Yasuda, 1957). The spiny process we observed on the rakers of *S. japonicus* probably form an even finer sieve than is formed by the rakers themselves. Regardless of the mode of selection (anatomical, behavioral, or perceptual), the selective capabilities of scombrids and coryphaenids would appear to be correlated with the anatomy of the gill raker apparatus.

An individual scombrid is able to prey on organisms differing greatly in size. It is capable of engulfing and retaining crustaceans, small fishes, and squid by means of a well-developed gill raker apparatus. It is also capable of pursuing, capturing, and ingesting fast-moving fishes and squids, provided they are not too large to be swallowed whole. The gill raker gap and maximum distensibility of the mouth and esophagus then would be expected to set limits on the range of food sizes eaten by scombrids. Within this size range a diverse faunal assemblage exists in the sea that includes numerous species of crustaceans, fishes, and molluscs. The diversity of species in the size range consumed by an individual scombrid has, to a great extent, masked the selectivity that does occur. The present paper provides some evidence for selection of organisms above a minimum size determined by the magnitude of gill raker gaps.

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The pole-and-line fishery for skipjack is the largest in the Hawaii fisheries. Average annual catches have been nearly 10 million pounds. Fishermen rely heavily on birds to signify that fish are present at or near the surface of the water.

Hawaii Fisheries

KEWALO BASIN IN HONOLULU is the main home of Hawaii's commercial fishing fleet and the site of its only cannery. The basin has a somber history. Kewalo can be translated as "the place of wailing." The name is well deserved. In the far past, unlucky Hawaiians who violated the tribal taboos (in Hawaiian, kapus) were taken there and drowned. But today Kewalo is a lively place. It is the spot from which the tour boats sail for Pearl Harbor. Brown amphibious Hawaiian boys dive for tourists' money. Docked there are catamarans that take visitors on moonlight sails past Diamond Head. Sleek white sport fishing craft wait for hire.

Rugged fishing sampans dock in Kewalo Basin next to the glittering tourist fleet. So far as artists are concerned, the sampans steal the show. A common sight at the basin is the painter with his easel trying to capture in oil the subtle faded colors of the sampans.

At one corner of the basin, its wide windows overlooking the busy scene, stands a fine seafood restaurant. Across the basin are the dockside research facilities of the Bureau of Commercial Fisheries Biological Laboratory. Its research vessels, *Townsend Cromwell* and *Charles H. Gilbert,* tie up there.

In some ways, Kewalo epitomizes the new Hawaii, a vigorous youthful State that is a happy blend of several cultures—Polynesian, Oriental, Yankee.

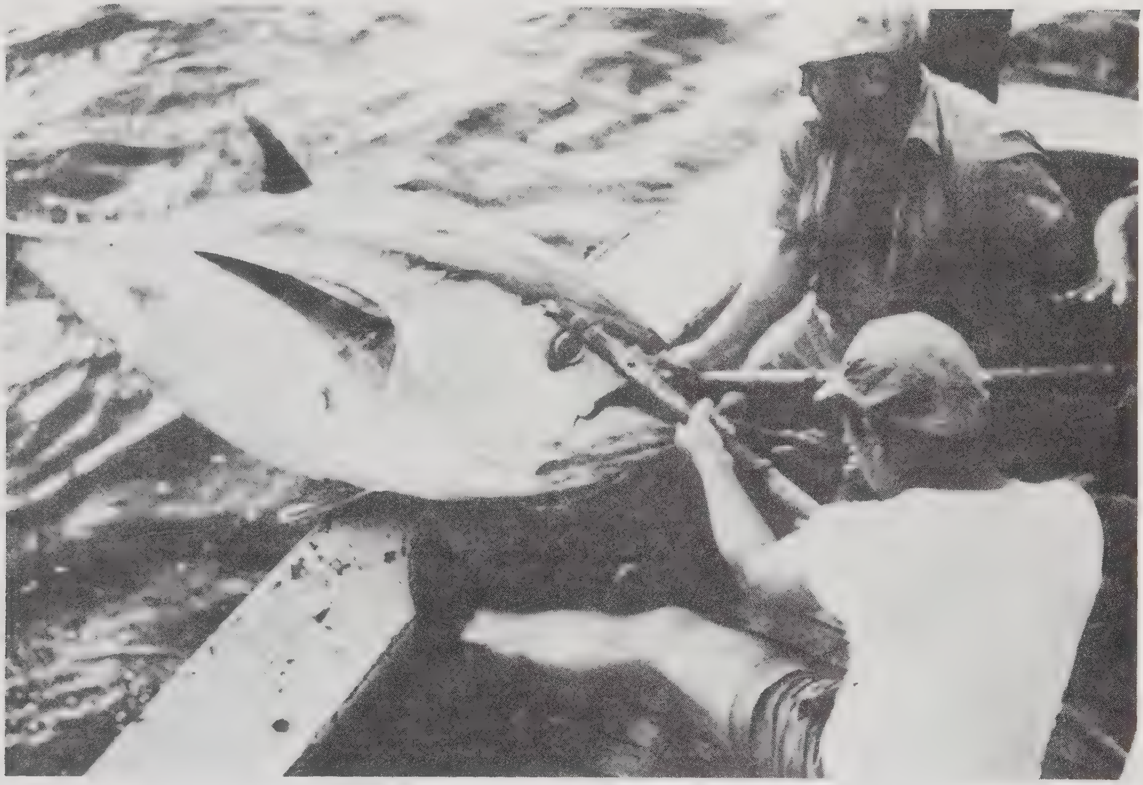
THE 20 ISLANDS OF THE HAWAIIAN CHAIN lie in an arc that runs 1,600 miles from northwest to southeast. Volcanic action formed the archipelago. The westernmost islands, worn nearly to the sea surface, are the oldest. Midway, best-known of the lee islands, is 1,300 miles northwest of Honolulu and only a few degrees from the International Date Line. It is a speck of land 2 miles square, whose highest point stands 43 feet above sea level. Hawaii, the largest, youngest, and southeasternmost of the islands, contains 4,021 square miles, and its peaks, Mauna Kea and Mauna Loa, rise 13,796 and 13,680 feet above sea level, high enough to wear a glistening coat of snow in winter.

The Hawaiian Islands rise steeply from a sea floor that averages about 3,000 fathoms (18,000 feet) deep. Fishing banks are few. The most notable is Penguin Bank off the western end of the island of Molokai, yet its 334 square miles provide little more than 1 percent of the Hawaiian catch. Off the coast of the island of Hawaii, one reaches 1,000-fathom water no more than 3 or 4 miles from shore.

Hawaii is just south of the Tropic of Cancer, at about the same latitude as Mexico City, Mecca, Calcutta, and Hong Kong. Raked by northeast trade winds, Hawaii is rarely oppressively hot and never cold. The average high temperature is about 78° F., the average low about 70° F. Sea surface temperatures are in the same balmy range.

Hawaii stands near the boundaries of two types of waters. To the northwest and often bathing the islands in the winter is North Pacific Central Water. This is warm and highly salty. To the southeast lies North Pacific Equatorial Water, warmer and far less salty. Between the two, and transitional between them in nature, is the west-flowing extension of the California Current. During summer, the entire State is often in the path of flow of the extension. Standing like stones in a stream, the islands set up a complex pattern of eddies in the current.

HAWAII FISHERIES MOSTLY HUG THE SHORE. About three-quarters of the catch is taken within 20 miles of the islands. The area fished in 1964 was about 24,000 square miles, a little larger than Lake Michigan. In that typical year, one-fourth of the commercial catch was made in two small areas, which together were only 4.3 percent of the entire area fished. Fishing areas are within easy distance of the two chief ports, Honolulu on the island of Oahu and Hilo on the island of Hawaii. There are no known biological or oceanographic reasons for these areas to be so much more productive than others; it appears they are so heavily fished because of their convenience. The most productive area—off the small town of Waianae,



Hawaii's fishing grounds are close to the main islands. The more important commercial species are shown in typical areas where Hawaiian fishermen operate. All fishing grounds for a species are not shown.

a few miles northwest of Honolulu—lies on the lee side of the island of Oahu and hence offers calmer seas.

The Waianae fishing grounds are immensely productive. In 1964, they provided a pelagic catch of about 7 pounds per acre, which seems to be a high yield for the open sea. The great Iceland Banks, for example, while immensely rich in bottomfishes (of which Waianae has few), supply 5.3 pounds per acre of pelagic fishes. The Samoa-based longline fishery for albacore in the South Pacific averages 0.009 pound per acre, or about 0.1 percent of the Waianae yield. On the other hand, the world's richest fishery, off Peru, yields about 400 pounds per acre.

THE FISHES OF HAWAII are, on the whole, common to most warm seas. A quick introduction to the Hawaiian language, a tongue that contains only 12 letters (7 consonants and the 5 vowels), can be gained by running through a list of the fishes landed commercially in the State. Kahala, akule, mahimahi, hapuupuu, aweoweo, opakapaka—it runs to more than 60 melodious names. The most famous Hawaiian fish, the humuhumunukunukuapuaa of the popular song, is not caught commercially. The fish fauna is less exotic than appears at first glance, for the names are the Hawaiian equivalents of more familiar English names.

The State of Hawaii, with 0.4 percent of the U.S. population, in 1968 provided

0.3 percent (12.9 million pounds) of the U.S. fish catch and 0.7 percent ($3.4 million) of its value. For the United States as a whole, the average price to the fishermen was 11.5 cents a pound. In Hawaii it was 26.8 cents.

Varied though the fishery resources are, five species of tuna and tunalike fishes account for most of the Hawaiian catch—80 percent by weight and 65 percent by value in 1968. The species are skipjack tuna (aku), albacore (ahipalaha), bigeye tuna (ahi), little tuna (kawakawa), and yellowfin tuna (ahi). These fishes have been caught throughout Hawaii's history. The first European visitors, late in the 18th century, described the canoe fishery for skipjack. Oahu's most famous landmark, Diamond Head, took its Hawaiian name—Leahi—from its resemblance to a tuna's dorsal fin.

Most of the elements of Hawaii's economy have boomed over the past two decades. Garment-making, for example, has grown from a handful of small shops to a $25 million a year industry, marketing vivid Hawaiian fashions on the mainland and in Europe and Asia. Tourism brought the State 15,000 visitors and $6 million in 1946; in 1967, about 1 million visitors spent $400 million.

But the fishing industry has failed to keep pace.

THOUGH SEVERAL METHODS OF COMMERCIAL FISHING are used in Hawaii, two techniques account for the bulk of the catch. These are pole-and-line gear, used to take skipjack, and longline gear, used to take bigeye and yellowfin tunas and marlins and other billfishes.

One species, skipjack, is the most abundant in the commercial catch. In 1965, a record year, skipjack constituted 82 percent of the total Hawaiian catch, by value 56 percent. In 1968, these percentages were 48 and 43.

In the skipjack fishery, the number of boats decreased from 32 in 1948 to 17 in 1966, the number of fishermen from 260 to 154. The average catch has remained at almost 10 million pounds—for only the most efficient fishermen have been able to operate and they have about doubled their efficiency. On the other hand, skipjack fishermen have had to work much harder by making more frequent trips than in the past.

In the longline fishery, the number of boats decreased from 59 in 1948 to 30 in 1966, the number of fishermen from 190 to 87. The catch has also declined, being little more than half what it once was.

THE SKIPJACK FISHERY had a prominent place in Hawaiian mythology. Kapus protected the fish at certain times of the year. The origins of the commercial catch are lost in history, but we know some of the first Japanese to reach the islands—shipwrecked fishermen rescued early in the 19th century by American whalers—earned their livelihood by fishing and selling skipjack.

John N. Cobb, in the first widely printed study of Hawaii's fisheries, reported a skipjack catch in 1900 of 401,053 pounds, valued at $41,383. The skipjack catch fluctuates widely. Since 1948 the smallest catch was made in 1957, when 6.1 million pounds were taken; the largest was 16.2 million pounds in 1965. The average catch is 9.9 million pounds. A cannery was built in 1940.

The craft used in the skipjack fishery are water-hugging wooden sampans between 60 and 80 feet long and 27 to 77 gross tons. A crew of 6 to 14 men is carried. A local anchovy (nehu) is the principal bait. A pound of nehu brings about

Sashimi—raw tuna red in color and sliced thin—is part of this attractive array of Japanese-style seafood and is popular with Hawaiians of Oriental descent and also many Caucasians.

40 pounds of skipjack. Nehu is seined in Pearl Harbor or other shallow areas.

Skipjack schools are usually located by sighting bird flocks. The vessel intercepts the school. The silvery nehu are thrown in the water to attract the skipjack to the stern of the ship. Water sprays are turned on. The fish are caught on unbaited barbless hooks and flipped to the deck. When skipjack are specially taken for the fresh-fish market, they are caught beneath the arm for unhooking, a method less likely to injure them. After a catch of sufficient size has been made (or as the day grows late), the ship heads for port. It makes a long day, for often the sampans will have spent predawn hours baiting before proceeding to sea to fish. The average catch per trip is about 6,000 pounds.

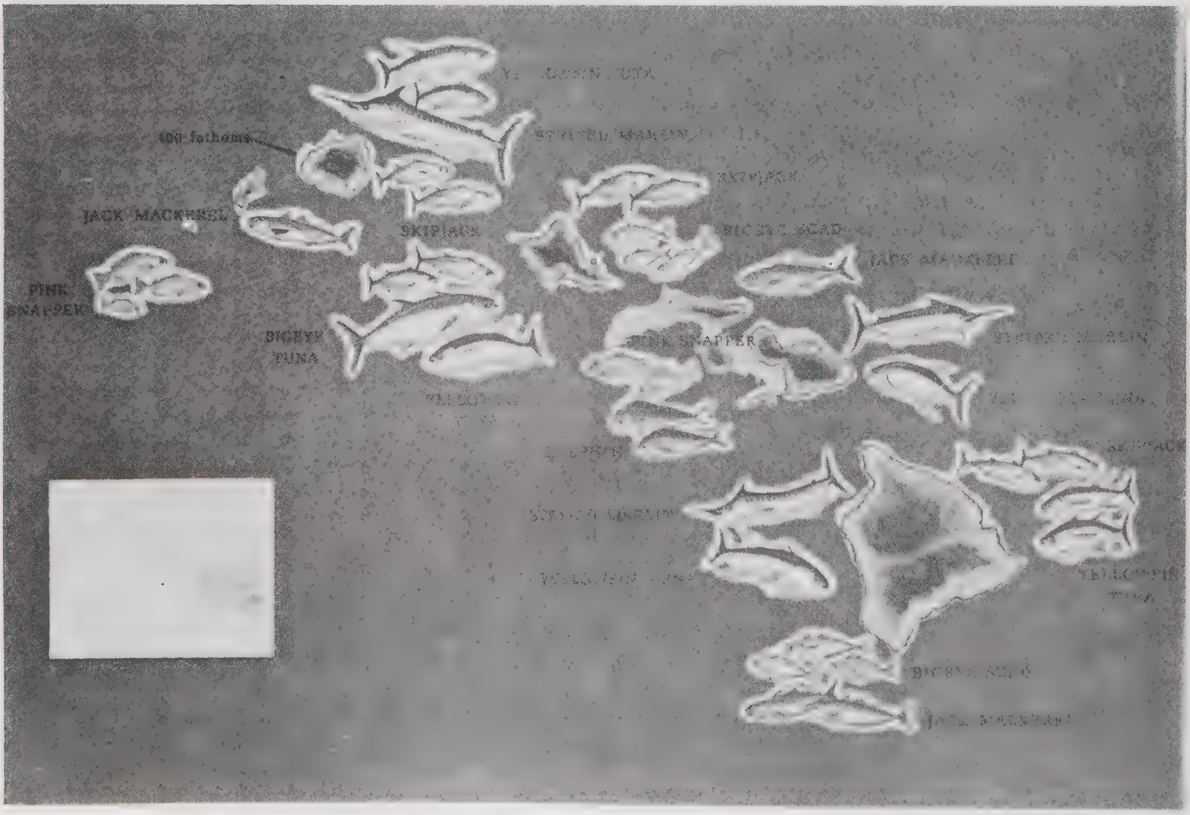
The need to fish for bait always reduces the time that might be spent scouting for skipjack. The nehu is a delicate fish and mortality in the live-bait tanks is high. Most students of the Hawaii fisheries agree that bait is one of the most critical problems faced by the industry. Recently, the Bureau of Commercial Fisheries has demonstrated that an introduced fish, threadfin shad, is an effective skipjack bait. As much as one-third of a fishing vessel's time is probably spent in baiting. Most of the rest of the time is spent in scouting. Actual fishing can occupy as little as an hour a day.

THE TUNA LONGLINE FISHERY is more recent than the skipjack fishery, having been introduced into the islands in 1917 by a Japanese immigrant. Hawaiian longliners, gear, and fishing techniques are scaled-down versions of the Japanese. A modern Japanese longliner, the kind that plies the waters of the central Pacific and often docks in Honolulu, will lay 50 miles of line at a set, a Hawaiian longliner 10 miles.

Most Hawaiian longliners remain close to shore. In the past few years, however, with the encouragement and advice of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, some have ventured several hundred miles south of the islands. They have been rewarded with catches substantially better than those made by their rivals on the traditional grounds. But not all Hawaiian longliners have the navigational equipment or the trained personnel to make the longer voyages. In 1969, a modern new vessel joined the fleet and has fished successfully far from the islands.

The longliners draw upon the same population of fishes—bigeye tuna, yellowfin tuna, albacore, and marlins and other billfishes—that help support one of the mightiest fisheries in the world, the Japanese longline fishery. The Japanese fleet has fished the Hawaiian area since 1953. Exact catch figures are not available, but estimates place the take at several times that of the small Hawaiian fleet. Thus, tunas may be caught 500 miles

Hauling aboard a bigeye tuna caught in Hawaii's longline fishery.

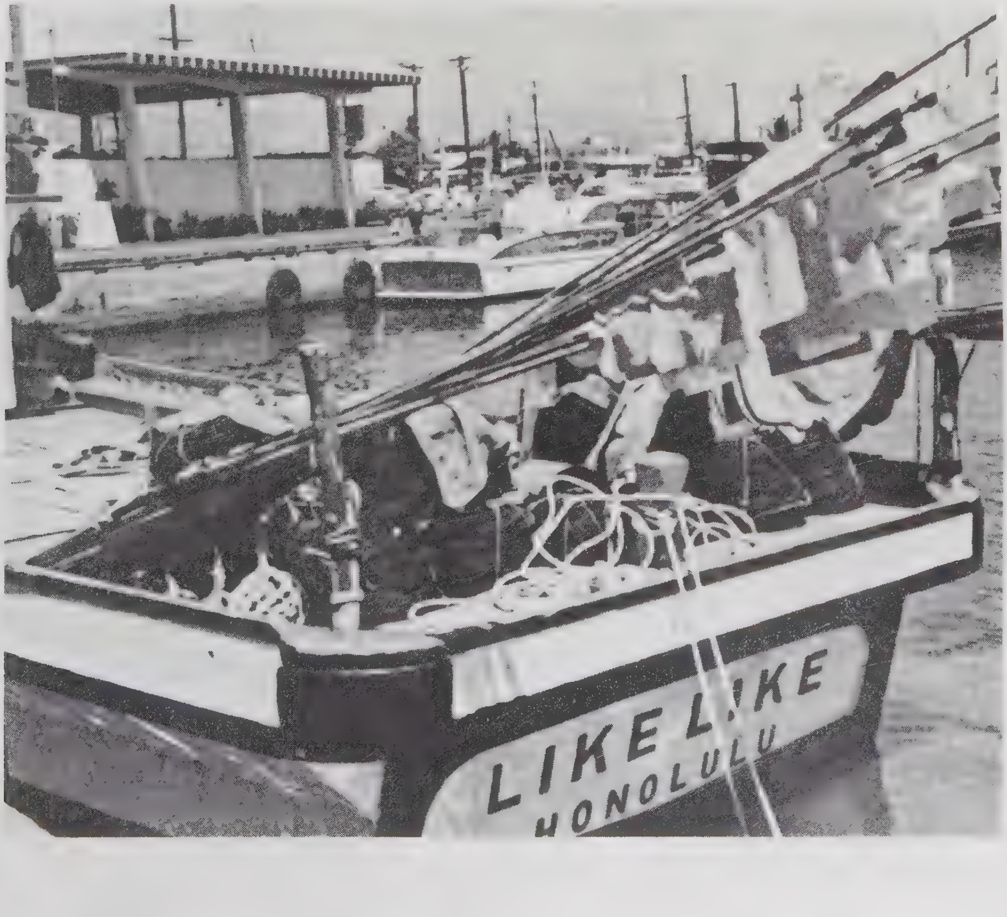


from Hawaii, shipped 3,400 miles to Japan, transshipped back to the U.S. mainland for canning, and (after still another sea voyage) wind up on the shelves of a Honolulu supermarket. The canned fish migrate distances as great as do the living fish.

OTHER HAWAII FISHERIES take a wide variety of fish and shellfish, some of which could be caught in larger amounts. The bigeye scad (akule) is an example. Typically, these dark-blue fish are about a foot long, although some grow larger. They are taken near shore with handlines and nets. Good fighters, the scad has been of increasing interest to sport fishermen. Catches of bigeye scad fluctuate widely. The year 1968 was very good and 898,770 pounds were caught. Another fish taken near shore with nets and handlines is the jack mackerel (opelu), much prized as a food fish. The catch in 1968 was 241,280 pounds.

The bottom fisheries provide several species for the Hawaiian dinner table. Among them are the snappers (uku, kalekale, opakapaka, ulaula, ehu, ulaula koae) and black sea bass (hapuupuu). About 252,000 pounds were landed in 1968. Like most fisheries for coastal species, the catch of snappers and sea bass

The gear aboard this Hawaiian longliner is used to take bigeye and yellowfin tunas and marlins and other billfishes from subsurface waters. Baited hooks are suspended at intervals along the buoyed longline, which may be 10 miles in length. Flags indicate the position of the longline in the water.



has declined since the early 1950's, when it was over 500,000 pounds annually.

Also declining are catches of the several species of jacks (ulua), closely related to the bigeye scad. The decline seems to reflect decreased commercial fishing effort rather than abundance of the fish.

Among the crustaceans, the spiny lobster once played a prominent part in Hawaii fisheries. In 1900, the catch was 131,000 pounds. The 1968 landings were about 4,520 pounds. The fishery is not intensive and rarely reaches depths below 15 fathoms. When the Honolulu Biological Laboratory leased the research submarine *Asherah* for operations off Oahu in 1965, scientists found large lobsters at depths of 50 to 65 fathoms. Lobsters this size are rarely seen, if at all, in the commercial catch.

Oysters were introduced into Hawaii in the 19th century and have become established. There are extensive beds in Pearl Harbor, but these waters are polluted, unfortunately, and no commercial catch is made. The Hawaii Division of Fish and Game is studying oyster cultivation. The venture has not yet attracted commercial interest.

One new marine product for export was added to Hawaii's slim list late in 1966. Precious coral was reported from the islands more than a century ago, but no effort had previously been made to harvest it. A small amount of precious coral is now taken between Oahu and Molokai. Fashioned into jewelry, it has enjoyed a good sale and a small industry appears to be in the making. The extent of the resource is unknown. Precious coral is found at great depths. Accessible to divers is the more plentiful and much cheaper black coral, which is fashioned into jewelry and widely sold.

A fishery traditional in Hawaii is the harvest from fishponds. The shores of the islands, particularly Molokai and Oahu, abound in stonewalled enclosures in which several species of food fish were once reared. Of the several hundred fishponds that have been mapped, only a handful are kept in repair and used, and these supplied about 12,000 pounds of fish in 1968. The milkfish (awa) was the most important, accounting for 50 percent of the 1968 harvest. Some scientists, notably those at the Oceanic Institute, are interested in putting the fishponds into wider use. Oyster-culture experiments have been conducted in one.

HAWAIIAN CONSUMPTION OF FISHERY PRODUCTS was once among the highest in the world. In 1900, the year the Republic of Hawaii became a Territory of the United States, the population was 150,000, one-fifth of what it is now. The total fish catch was 6.2 million pounds, or about one-half to one-third that of today. The entire 1900 catch was consumed locally, yielding about 41 pounds (round weight) per capita, a figure that is above present average U.S. consumption and approaches that of Asian countries. In 1968, the per capita consumption of locally caught fish was around 8 pounds. The change between 1900 and 1968 reflects shifting cultural tastes, rather than reduced productivity of the sea.

Locally caught fish are only a part of the fish and shellfish eaten in Hawaii. In 1963, for example, about a pound of shrimp per capita was imported from foreign sources alone. How much shrimp is shipped from the U.S. mainland is not known. The import of marine products is not new, by the way. It started almost as soon as the outside world discovered the Hawaiian Islands. Salted salmon from the

Pacific Northwest immediately became a staple in the Hawaiian diet and remains so to this day. Old records disclose that in 1900 the new Territory imported 757 pounds of salted salmon eggs (caviar), which wholesaled at the remarkably low price of $1.28 a pound.

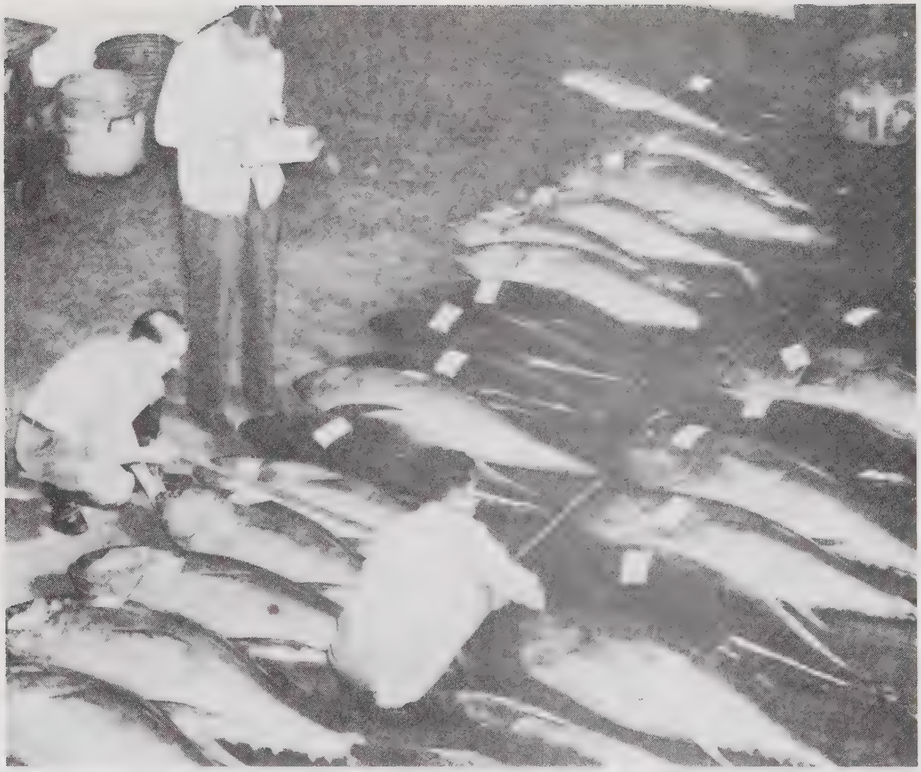
No reliable estimates of total Hawaiian consumption of fishery products have been made. Polynesians and Orientals have many delicious and unusual ways of preparing fish and other seafoods. Because many of her citizens are of Polynesian or Oriental descent and because many of their dishes have been adopted with relish by Caucasians, Hawaii's actual consumption per person is probably considerably higher than the 8 pounds cited above.

Some seafoods that appear regularly on the Hawaiian dinner table, regardless of the family's ethnic background, are usually available in only a handful of specialized and expensive restaurants on the mainland. This is notably true of sashimi. Sashimi consists of thin slices of chilled tuna or other seafood. It is eaten raw after being dipped in a pungent mixture of soy sauce and grated hot radish.

Akin to sashimi, and also very popular, is sushi, another Japanese delicacy. The basis of sushi is a ball of cold rice that has been marinated in a weak solution of vinegar, salt, and sugar. This is brushed with fiery green horseradish and a slice of raw fish is laid on top.

Kamaboko—Japanese fishcake—is often served. One form is a white gelatinous fish loaf with a brilliantly colored outer layer. Sliced thin, kamaboko is arranged

Seining for small fish that will be used as live bait in the skipjack fishery. Nehu, an anchovy, is the most sought-after bait. It is thrown into the water to attract skipjack close to the vessel where they can be caught with pole and line and unbaited barbless hooks.



Tunas from the longline catch are sold at the auction market in Honolulu. Bureau scientists are recording data for life history and population studies. In right foreground are several marlins.

on lettuce or shredded cabbage and served cold as a side dish. Kamaboko is an integral part of several Oriental dishes and is also served as a pupu, as appetizers are called in Hawaiian.

Among the Chinese specialties are lobster in black bean sauce, steamed mullet, and half a dozen other commonly served dishes, particularly those using shrimp.

Unfamiliar to most mainlanders is the opihi, a limpet about the size of a dime; it is eaten raw. A great delicacy among the Hawaiian people, opihi cling to rocks at the water's edge. In 1968, the more than 5,000 pounds of opihi that reached the market brought the fishermen the substantial average of $3.54 a pound. The 1900 catch was more than 140,000 pounds.

Another Hawaiian delicacy, the opae, is rarely seen in markets or on restaurant menus because the catch is small—496 pounds in 1968. The opae is a fresh-water shrimp about 1½-inches long. It is boiled and eaten whole.

The Hawaiians also have a raw-fish dish. This is poki, chilled and cubed raw skipjack tuna, which is marinated in spicy sauce that includes the local kukui nut. Two of the most widely available Hawaiian dishes make use of imported fish—lomi salmon (salted salmon, fresh

Hawaii's fisheries produce a colorful array of fish for the local fresh market.

tomatoes, and green onions) and lau lau (butterfish and pork wrapped in taro leaves and baked in an imu, or underground oven).

A study in 1967 of the food preferences of Hawaiian families showed that 6 of the 10 most popular ethnic dishes contained seafood. They were the Chinese pohloh ha (pineapple and shrimp), Japanese shrimp tempura (fried shrimp with batter), Japanese sashimi (raw fish), Hawaiian lau lau (pork, butterfish, and taro leaves), Japanese kamaboko (fishcake), and Chinese ha chok kailan choy (shrimp with broccoli). Any good Hawaiian cookbook can provide these and many more novel seafood dishes to enliven mainland menus.

Almost all visitors to Hawaii are introduced to the dolphin, a fish locally called mahimahi. In 1968, about 70,000 pounds were landed in Hawaii, enough to give each visitor about 1 ounce. Mahimahi is locally popular, too, and much of it is imported from Japan. The dolphin has never been the sole object of a fishery in Hawaii, being taken incidental to other catches. Two fishes taken in far greater abundance—the jack mackerel (opelu) and bigeye scad (akule)—the visitor will not often see, but both play a role in the Hawaiian diet.

THE CHIEF FISH MARKETS in Honolulu lie at the edge of Chinatown, where a number are clustered in a single large building. There are several neighborhood fish markets in the city, and almost each of the small grocers may carry a few fresh fish. The supermarkets offer several varieties of fresh seafoods. Retail prices are high. Locally caught fish are about $1 a pound. Around New Year, premium tuna for sashimi will retail for as much as $5 a pound.

The cannery in Honolulu is one of the production facilities of Bumble Bee Seafoods, a division of Castle and Cooke. One of the oldest firms in Hawaii, Castle and Cooke is now among the largest corporations in the United States. The Honolulu cannery employs about 275 people, processing 40 to 50 tons of tuna a day. Canned tuna, the principal product, is sold locally and on the mainland. Such byproducts as fishmeal, fish solubles, and canned pet foods are also manufactured. The cannery operates an ice plant (the largest in Honolulu) and a shipyard.

Kamaboko is only one form of fishcake produced in Honolulu. Fish, usually black marlin, are steamed, and cornstarch and seasoning are added. The cake is molded mechanically into a cylindrical roll. Red vegetable dye is used to color the outer part. Chikuwa, another form of fishcake, also uses marlin as its base, but the cake is broiled. Tempura fishcake, a mixture of yellowfin tuna, bonefish, snappers, and other fish, is seasoned with carrots and burdock and then deep-fried. There are five manufacturers of fishcake in Hawaii.

A smaller industry is engaged in processing dried fish. Skipjack tuna is favored. It is prepared in the form of lamp-dried sticks—with no seasoning other than salt—or is soaked in soy sauce and spices and then dried.

Filipino fish sauce, bagoong, is also made in Honolulu. Skipjack tuna is its base. Bagoong, like many of the sauces of Southeast Asia, consists of fish which has been fermented; it is widely used as a seasoning and is a good source of protein.

None of these products has found wide acceptance on the mainland as yet, but are of sufficiently high quality and exotic appeal to make their way eventually to at least the gourmet sections of mainland markets.

THE PICTURE DRAWN THUS FAR is of a small State with few natural fishery resources that give any promise of broadening the economic base greatly. This is not necessarily correct. Thanks to intensive fishery research, it appears that Hawaii may be in a position to become one of the great fishing states.

Research on the fishes and fisheries of Hawaii is conducted by four agencies.

The Federal Government was first in the field. Pioneering research was done by the great ichthyologist, David Starr Jordan, his associate, Barton Warren Evermann, and fishery biologist John C. Cobb at the time of annexation.

In 1947, the U.S. Congress passed the Farrington Bill, which directed the Secretary of the Interior to conduct fishing explorations and related oceanographic, biological, technological, statistical, and economic studies to insure maximum development and use of the high-seas fish-

Hawaiian tuna longliners often take billfishes, such as this huge black marlin, which will be used to prepare kamaboko, or Japanese fishcake.

ery resources of the territories and island possessions of the United States in the tropical and subtropical Pacific Ocean. The Pacific Oceanic Fishery Investigations, now the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, was established under this authorization in 1948.

The laboratory is widely known for its discovery of yellowfin tuna stocks in the equatorial Pacific and of skipjack tuna in the Marquesas Islands; for its elucidation of the complex pattern of transpacific migration of albacore in the North Pacific; its work on the physiology and behavior of tunas; and its pioneering oceanographic studies of the central Pacific. Its principal mission today is bringing into production the great skipjack tuna potential of the central Pacific. To this end it is conducting work on the local Hawaiian skipjack tuna fishery, and on the subpopulations of skipjack tuna in all parts of the Pacific Ocean. It is investigating the movements of tunas underwater by use of a complex sonar on its research vessel *Townsend Cromwell.*

Aiding the local industry, and likely to be called upon more heavily if substantial development takes place, is the loan fund administered by the Bureau of Commercial Fisheries. Sixteen loans, totaling $219,868, have been approved. These were for such items as purchase of new equipment, replacement of a vessel, and vessel repairs. Other requests for loans are pending.

The Division of Fish and Game of the Hawaii Department of Land and Natural Resources came into being in 1919 with the establishment of a Territorial Fish and Game Commission. Through World War II it confined itself largely to law enforcement, beginning scientific studies only about 20 years ago. Substantially assisting the research programs of the Hawaii Division of Fish and Game are matching funds provided by the Federal Government through the Bureau of Commercial Fisheries under the Commercial Fisheries Research and Development Act.

Funds of more than $150,000 are supporting studies on the handling of bait fish; growth and migratory behavior of the bigeye scad; biology of the kona crab; statistics of the spiny lobster catch; development of a commercial oyster industry; and development of a prawn (shrimp) fishery, the prawn (*Macrobrachium rosenbergi*) being one common in Southeast Asia. The Division has been so successful in cultivating *Macrobrachium* that its work has attracted wide attention among fishery biologists in Southeast Asia.

The University of Hawaii, founded in 1907, has conducted basic research on fishes for many years. Its widely known Hawaii Institute of Marine Biology, with its laboratory on Coconut Island (off Oahu), has been in operation since 1922. An Institute of Fisheries was founded in 1965. Federal funds, some available under contracts with the Bureau of Commercial Fisheries, have contributed heavily to the University's expanded marine research.

A private foundation, The Oceanic Institute, began operations in 1964. The institute is a part of the Makapuu Oceanic Center, an ocean science and technology complex, which also includes the beautiful and popular Sea Life Park, a science-oriented public marine exhibit whose proceeds help endow scientific programs. The Oceanic Institute is studying such problems as brackish-water fish culture and the behavior of whales, porpoises, and dolphins.

CONCERNED BY THE SLUGGISH ECONOMIC PACE OF THE HAWAII FISHERIES, the State Legislature in 1965 asked the Governor to convene a conference of experts to assess the potential of the central Pacific. A group of 12 scientists reviewed all available literature and drew up a series of reports. Key sections of these reports, submitted to the Governor's Conference on Central Pacific Fishery Resources, dealt with estimates of potential tuna catches. The working groups found that—if yellowfin tuna could be caught at younger ages than are now taken by the Japanese longline fleet—an increased catch of about 110 million pounds a year would be possible. This would have boosted the total 1964 U.S. yellowfin tuna catch by nearly 75 percent. Large bigeye tuna, it was concluded, are now being fished by the Japanese longline fleet at or above the maximum sustainable yield and no increase is foreseen. But skipjack, mainstay of Hawaii's industry, has an enormous potential.

Creatures of the warm seas, skipjack are harvested by the United States in the Atlantic (although only a few are taken at present), in the eastern Pacific, and in the central Pacific.

The skipjack taken near the shores of the Americas are small, young fish. Evidence suggests that these young fish are migrants. One of the most telling pieces of substantiating evidence is that, although intensive surveys have been conducted off North and South America for years, only a handful of skipjack larvae have ever been collected. Yet, near Hawaii the larvae are the most plentiful of all tuna larvae collected so far, and are found at many other places west of about longitude 130° W. It is believed that skipjack spawn in the equatorial central Pacific and then the young migrate from the south and west into the eastern Pacific fishery. After remaining there no more than a few months, the fish move westward again to spawn. Some undeniably enter Hawaiian waters. Three skipjack tagged in the eastern Pacific have been retrieved many months later in the Hawaiian catch.

What is the size of the central Pacific skipjack resource? Estimates vary; some place the yield at about 295 million pounds a year. If these fish could be caught, they would boost skipjack to first place in the U.S. tuna fisheries.

Thus, a resource of enormous potential value exists in the central Pacific. The question is—how to harvest it? In the eastern Pacific, skipjack are taken with purse seines. In the 1950's, efforts to use this gear in Hawaii were unsuccessful, but there have been so many developments in gear and techniques that scientists are urging new long-term trials to harvest this resource.

THE DRIVE TO IMPROVE HAWAII'S FISHERIES appears likely to follow two lines. First, the State Government is seeking to outline a long-range development plan for existing fisheries, one that would inject new life into the present industry. Second, increasing effort may be thrown behind the drive to solve the scientific and technological problems that stand in the way of harvesting the latent skipjack resource fully.

Hawaii's fisheries are now small, colorful, and not as prosperous as they might be. But as with so many things in this young and energetic State, they hold promise of contributing materially to the future economic welfare of the Hawaiian people.

And as is also true with the other facets of the State's growth, something valuable and attractive may have to be sacrificed if the fisheries are developed. Certainly doomed by any major development would be Kewalo Basin, with its blend of Hawaii's several cultural strains and its echoes of the past. It is far too small to house a larger fleet. But this is a choice Hawaii or any other developing community faces and solves perpetually.

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7136

EFFECTS OF DELAYED INITIAL FEEDING ON LARVAE OF THE GRUNION, *Leuresthes tenuis* (AYRES)

Robert C. May[1]

ABSTRACT

The initial feeding of newly hatched larvae of the grunion, *Leuresthes tenuis* (Ayres), was delayed for various periods of time under laboratory conditions at 18° C. Unfed larvae did not develop morphologically beyond the stage reached at the time of yolk absorption, about 4 days after hatching, although some survived as long as 3 weeks. Regardless of how long initial feeding was delayed, 80% or more of previously unfed larvae began feeding when food was made available to them, and at least 40% of the larvae alive when food was offered were able to survive to the end of a 20-day experiment. Some larvae feeding for the first time after 1 to 2 weeks without food, died after gorging themselves with *Artemia* nauplii. When food was offered to starved larvae, growth began and generally proceeded at about the same rate as in larvae fed from day 1, although there was some indication that a few days' delay in initial feeding increased the conversion efficiency of grunion larvae feeding on *Artemia* nauplii. Catabolism of fat provided most of the energy for metabolic processes during starvation. The condition factors and carbon/nitrogen ratios of unfed larvae were below those of fed larvae; condition factor seemed to be the better index of nutritional state. Grunion larvae probably do not experience high mortality at sea due to starvation, nor do they exhibit a classical "critical period" at the time of yolk absorption.

Most marine fishes pass through a free-swimming larvae stage, and it is well documented that survival through this stage is very low, generally being much less than 0.1% (e.g., Sette, 1943; Ahlstrom, 1954; Pearcy, 1962; Iizuka, 1966). The rate of survival through the larval stage is probably the most important factor determining the strength of year classes (Beverton, 1962; Gulland, 1965). Hjort (1914, 1926) advanced the hypothesis that larval survival was drastically affected by the abundance of food at the time the yolk was completely absorbed, and that poor year classes resulted when insufficient food was available to larvae at this "critical period." As Marr (1956) pointed out, Hjort's "critical period" concept has had a profound effect upon the thinking of fishery biologists.

Increased larval mortality at the time of yolk absorption has, however, proved difficult to demonstrate in nature. Marr (1956) concluded that the published evidence did not establish the existence of such increased mortality at sea; even in the light of more recent field data (Farris, 1961; Pearcy, 1962; Stevenson, 1962; Iizuka, 1966; Karlovac, 1967), it is difficult to decide from survival curves whether increased mortality at yolk absorption does in fact occur in nature. It has proved equally difficult to demonstrate that starvation is a major cause of larval mortality in the sea. Wild larvae found with empty guts (Lebour, 1920; Bowers and Williamson, 1951; Arthur, 1956; Bhattacharyya, 1957; Berner, 1959) may indicate imminent death by starvation or may reflect artifacts such as defecation or selective capture by plankton nets (Blaxter, 1965, 1969). Reports of apparently emaciated larvae, sometimes caught in regions where food is scarce (Soleim, 1942; Arthur, 1956; Shelbourne, 1957; Nakai, 1962; Hempel and Blaxter, 1963; Nakai et al., 1969), are suggestive but inconclusive (Marr, 1956; Blaxter, 1965, 1969). Field data thus indicate the possibility of high larval mortality due to starvation after the yolk has been absorbed but have not demonstrated its existence conclusively

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or determined its significance for year-class strength.

The response of larvae to food deprivation in the laboratory may provide badly needed evidence of how susceptible they are to starvation at sea. There have, however, been few attempts to determine experimentally the effects of delayed initial feeding on the larvae of marine fishes. Fabre-Domergue and Biétrix, the two pioneers of marine fish culture who coined the term "critical period," which Hjort later adopted, believed that feeding before the yolk supply was exhausted was essential to assure larval survival in laboratory rearing attempts. They stated that among larvae which received food prior to yolk absorption, ". . .*la phase que nous avions nommée période critique post-larvaire n'existe pas*" (Fabre-Domergue and Biétrix, 1898: 468). These authors went on to say that larvae which did not receive food early would subsequently become weak and unable to capture food and would exhibit considerable, if not total, mortality (Fabre-Domergue and Biétrix, 1898). The importance of early feeding for marine fish larvae was not further investigated in the laboratory until Blaxter and Hempel (1963) studied the effects of delayed initial feeding on the behavior of larval herring, *Clupea harengus* L. By feeding larvae after successively longer times without food, Blaxter and Hempel determined the time beyond which the larvae failed to exhibit feeding movements when supplied with food, a time they called the "point of no return." This point came 5 to 9 days after complete yolk absorption, at temperatures of 12° to 8° C, much later than the statements of Fabre-Domergue and Biétrix would have led one to expect. Recently, Lasker et al. (1970) observed the mortality of larvae of the northern anchovy, *Engraulis mordax* Girard, which had been fed at progressively later times after hatching. At temperatures of 15° to 22° C, larvae for which initial feeding had been delayed until 2.5 days after complete yolk absorption, showed the same pattern of mortality as groups of starved controls, while larvae receiving food 1.5 days after yolk absorption exhibited good survival—a phenomenon which these authors termed "irreversible starvation."

The purpose of the present study was to investigate in detail the changes which take place in starving larvae and in larvae whose initial feeding is delayed for various lengths of time, and thus to bring more evidence to bear upon the perennial questions of how susceptible larval fishes are to food deprivation and whether they do pass through a "critical period" at the time of yolk absorption. This study also sought to broaden the range of our knowledge of larval fish ecology by utilizing a species belonging to a group other than the Clupeiformes or Pleuronectiformes, or which nearly all of our information has hitherto been based. The fish chosen for study was the grunion, *Leuresthes tenuis* (Ayres), a member of the family Atherinidae. Atherinids produce rather large demersal eggs (Breder and Rosen, 1966), and the well-developed larvae which hatch provide an interesting contrast with flatfish and clupeoid larvae. Specifically, these experiments were designed to determine the effects of delayed initial feeding on mortality, on growth, and on the ability of grunion larvae to begin feeding and to utilize ingested food, and to ascertain what changes in the morphology and chemical composition of the larval body occur during starvation.

MATERIALS AND METHODS

SOURCE OF EGGS; HATCHING

The grunion is best known for its unusual habit of spawning on the sandy beaches of southern California and northern Baja California (Thompson and Thompson, 1919; Walker, 1952; Breder and Rosen, 1966). The eggs are deposited in the sand at night at certain times in the tidal cycle and are washed free some days later by a succeeding high tide, at which time the larvae hatch if the developmental period has been sufficiently long. The spawning season extends from late February or early March to late August or early September, with spawning intensity reaching a peak in April and May (Walker, 1952). During this time it is relatively easy to collect grunion eggs, which therefore provide convenient material for the study of embryonic and larval development.

Eggs for the present study were collected during a spawning run on the night of March 24, 1970, at the beach in front of Scripps Institution of Oceanography, La Jolla, Calif. The eggs from a running ripe female were expressed into a small plastic container and artificially fertilized by adding milt from one male and a small amount of seawater; after approximately 1 min the water was decanted and sperm removed with several washes of fresh seawater. At the National Marine Fisheries Service Fishery-Oceanography Center in La Jolla, developing eggs were dispersed in a layer of washed, slightly moist beach sand approximately 1 cm deep at the bottom of rectangular plastic containers (16 × 12 × 11 cm), and a paper towel moistened with seawater was placed on the surface of the sand. The tops of the containers were covered with aluminum foil. This incubation procedure, essentially the same as one described by Morris (1956), kept the eggs moist and produced good hatching when excess water (which quickly brought on anoxic conditions) was avoided. The containers were placed in a water bath held at 20° ± 1° C by manually mixing water from the warm and cold seawater systems of the Fishery-Oceanography Center (see Lasker and Vlymen, 1969). The day before hatching, the temperature of the water bath was lowered to 18° C over a period of 3 hr.

On April 3, 1970, after 10 days of incubation (a common incubation time in nature, according to Walker, 1952), hatching was induced by adding filtered seawater at 18° C to the incubation containers and agitating the water and sand by drawing water rapidly in and out of a pipette. Hatched larvae were immediately transferred via pipette (4-mm bore) to 18° C water in rearing containers. In this paper the day of hatching will be referred to as day 0, the day after as day 1, and so forth.

DESIGN OF EXPERIMENT

A total of 20 rearing containers was set up, each with approximately 50 newly hatched grunion larvae. Seven containers (#1-7) were used to determine the effect of delayed initial feeding on mortality and growth; in six containers in this group, feeding was begun at progressively later times at 3-day intervals beginning on day 1—i.e., on days 1, 4, 7, 10, 13, and 16—while the larvae in one container (#7) were not fed and served as a control. On the 20th day after hatching, all surviving larvae which had received food in this series were collected, and the length, weight, and chemical composition of the larvae were determined. Seven of the other containers (#8-14) were fed daily beginning on day 1, and six (#15-20) were given no food; these containers, referred to as "supply containers" in what follows, supplied fed and unfed larvae for measurements of length, weight, and chemical composition and also for experiments on feeding and growth. On the same days when feeding was begun in a new container in the delayed feeding series (containers #1-7), larvae from both the "fed" and the "unfed" supply containers were used to determine the incidence of feeding and to begin quantitative feeding experiments.

PHYSICAL CONDITIONS

Water of approximately 33 ‰ salinity was taken from the seawater system of the Fishery-Oceanography Center. The larval fish containers were originally filled with HA Millipore-filtered seawater, and at weekly intervals filtered water was added to the fed containers in order to replace water removed with uneaten food and fecal matter (see below), the volume added usually being between 1 and 2 liters. The temperature in the water bath was kept at 18° ± 1° C, and temperatures in the larval containers were within 0.5° C of the bath temperature. Eighteen degrees is the midpoint of the 14°-22° C range of water temperatures which occurs off La Jolla during the spawning season of the grunion (Reid et al., 1958). Banks of two 40-watt "daylight" fluorescent lamps positioned 76 cm above the surface of the water illuminated the containers for 12 hr each day. The lights were timed to go on after sunrise, so that diffuse light entering through windows increased slowly in intensity as the sun rose and no abrupt dark-light transition was imposed upon the larvae.

CONTAINERS

The containers used for rearing larvae in this study were the same as those described by Lasker et al., 1970), being circular (35 cm diameter, 14 cm deep) and made of the plastic alloy Kydex.[2] These containers have nonglossy black surfaces and hold 10 liters of seawater. For feeding studies with individual larvae, smaller Kydex containers were used (10.5 cm diameter, 4.2 cm deep) which held 300 ml of water. Both large and small containers were covered with clear plexiglass tops to reduce evaporation and keep out dust particles.

FEEDING

Nauplii of the brine shrimp, *Artemia salina*, were used exclusively as a food source. *Artemia* nauplii have proven to be poor food for larval clupeids but excellent for several other types of larvae (May, in press), and they appear to satisfy the nutritional requirements of larval grunion. Nauplii were obtained by hatching San Francisco brine shrimp eggs in trays modeled after those described by Riley (1966). Two trays were used, which allowed harvesting of trays on alternate days with a time lapse of 48 hr between inoculation of eggs and harvesting of nauplii. The water in the trays was kept at about 20° C. Nauplii were rinsed in filtered seawater and added to rearing containers shortly after the lights went on each morning, and more were added during the day if the concentration dropped low enough to prevent *ad libitum* feeding. If any uneaten nauplii remained from the previous day, as many as possible were removed by pipette before the morning addition of new nauplii. Fecal matter was siphoned daily from the bottoms of the "fed" containers.

QUANTITATIVE FEEDING STUDIES

At 3-day intervals beginning on day 1, 6-day quantitative feeding experiments were begun to measure the food consumption and growth of previously fed and unfed larvae. Larvae were transferred individually, from both the "fed" and the "unfed" supply containers, to small (300 ml) containers late in the afternoon on the day before the beginning of the feeding experiment. Three larvae from a "fed" container and three from an "unfed" container were used in each feeding experiment; individual larvae were kept in separate containers during the feeding study.

On the morning following transfer to the feeding containers, and for six mornings thereafter, a known number of *Artemia* nauplii was counted out with a pipette under a dissecting microscope and added to each container. Shortly before the lights went off at the end of the day, the grunion larvae were transferred by pipette to new containers, and the uneaten *Artemia* in the old containers were concentrated on a nylon mesh, preserved in Formalin and later counted. The difference between the number of nauplii added in the morning and the number left at the end of the day gave the number eaten by a larva. At the start of the series of feeding experiments, on day 1, 100 nauplii were added to each experimental container; when larvae consumed 70% or more of the nauplii offered, the number offered the following day was increased by 50 nauplii. On the morning following the final (6th) day of feeding, the experimental larvae were collected and analyzed as described below. The weight of a larva at the start of the feeding experiment, estimated from the mean weight of 10 larvae sampled at that time, was subtracted from the weight of the experimental larva at the end of the feeding period to yield its gain in dry weight.

In order to determine the weight of the ingested material, the weight of a single *Artemia* nauplius was estimated by making several weighings on an electrobalance[3] of groups of 5 to 20 nauplii, collected at the same interval after inoculation of eggs as the nauplii used in the feeding study. The nauplii were rinsed with distilled water and dried to constant weight at

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[2] Kydex is manufactured by Rohm and Haas, Philadelphia, Penn. Use of trade name does not imply endorsement of the product.

60° C before weighing. The mean weight per nauplius was 1.64 μg, almost identical to Paffenhöfer's (1967) value of 1.65 μg per newly hatched *Artemia* nauplius. Where the larvae had yolk sacs at the beginning of the feeding period, the mean weight of the yolk masses dissected off the 10 larvae sampled at the start of the experiment (the dissection technique is described below) was added to the weight of the nauplii consumed to yield the total dry weight of the consumed material.

The growth and food consumption of individual larvae during the feeding period were thus known and allowed calculation of the efficiency of food conversion:

$$\text{percent conversion efficiency} = \frac{\text{dry weight gained}}{\text{dry weight consumed}} \times 100.$$

INCIDENCE OF FEEDING

The percentage of larvae which fed after progressively longer times without food, termed here the incidence of feeding, was determined in separate experiments in 10-liter containers. Approximately 25 larvae were transferred from one of the "unfed" supply containers to a 10-liter container with filtered seawater late in the afternoon preceding the experiment, and on the following morning large numbers of *Artemia* nauplii were introduced into the container. One hour later, the anesthetic MS-222 (tricaine methanesulfonate) was added to the container to a concentration of 132 mg/liter, and the anesthetized larvae were examined under a dissecting microscope for the presence of an orange-colored gut indicative of feeding on *Artemia* nauplii. Simultaneously, the incidence of feeding among larvae from one of the "fed" supply containers was determined in the same way, to serve as a control with which hitherto unfed larvae could be compared. Experiments of this sort were conducted on the same days on which food intake and conversion experiments were started, beginning with day 4. Owing to mortality from starvation, the numbers of larvae available in the "unfed" containers dwindled so that only 13 larvae were available for the feeding incidence experiment on day 13 and 4 on day 16. By day 16, body pigmentation had developed in larvae from the "fed" containers to such an extent that feeding incidence could not be assessed by examining the coloration of the gut, and no value was obtained for previously fed larvae on this day.

Anesthesis stimulated peristalsis in grunion larvae, as Blaxter (1965) observed in larval herring, but the procedure in the present experiment was rapid enough that at most only the contents of the rectum were being extruded during examination and all larvae which had in fact fed were recorded as such. It should be pointed out that, unlike the straight, tubelike gut of clupeid larvae, the gut of larval grunion is already differentiated at hatching into three more or less distinct portions, the last of which, the rectum, is separated from the rest of the gut by an "ileorectal valve" (Al-Hussaini, 1947) which inhibits rapid defecation of material not in the rectum.

MORTALITY

Dead larvae were removed from the containers each morning by pipette. A larva was considered dead when its brain had become opaque and it did not respond to water current or to tactile stimulation. Dead larvae were routinely examined with a dissecting microscope.

SAMPLING PROCEDURE AND ANALYSIS OF LARVAE

Larvae were collected by pipette, and their lengths measured with an ocular micrometer from snout to tip of notochord, or, after upward flexion of the tip of the notochord had taken place, to the posterior edge of the hypural elements (standard length). Only free-swimming larvae were sampled, although in "unfed" containers these became increasingly rare toward the end of the experiment. Sampled larvae were rinsed quickly in distilled water and placed on glass microscope slides. Since larvae which were sampled on days 1 and 4 still possessed yolk sacs, they were preserved in 3%

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[a] Cahn Instrument Company, Paramount, Calif.

Formalin (in 50% seawater). Within 1 week of sampling they were rinsed in distilled water and their yolk dissected off, separated larvae and yolk masses being placed on microscope slides. The samples on slides were dried to constant weight at 60° C and weighed to the nearest microgram on an electrobalance. In agreement with the results of Blaxter and Hempel (1966), no effect of Formalin on the dry weight of larvae was found, nor was there a significant effect of Formalin on the dry weight of yolk masses (this was tested in a previous experiment by comparing dry weights of yolk dissected from preserved larvae with yolk dissected from frozen larvae or collected in preweighed capillary tubes).

Larvae sampled from the supply containers at 3-day intervals, and those collected from the delayed-feeding series on day 20, were analyzed for their ash, carbon, hydrogen, and nitrogen content. Percent ash was determined by weighing separately three randomly chosen larvae from each sample before and after combustion at 500° to 520° C. In the case of larvae fed from day 16 and sampled on day 20, only one larva was available for the ash determination. During combustion, larvae were held on tarred pieces of precombusted aluminum foil, and weighings were made on an electrobalance. The remaining larvae in each sample were ground into fine particles with an agate mortar and pestle, and two aliquots of this material from each sample were analyzed for carbon, hydrogen, and nitrogen content with a Model 185 carbon-hydrogen-nitrogen analyzer.[4] The number of replicates was limited by the amount of material available, but variation between replicate determinations was small, and means calculated from the replicates were accepted as the ash, C, H, and N values for the sample. This approach to the chemical analysis of larvae was chosen because it allowed determination of C/N ratios, estimation of protein and fat content, and calculation of caloric content (see Results section).

Larvae which had been used in the feeding incidence experiments described above were preserved in 3% Formalin and later cleared in KOH and stained with Alizarin Red-S, the standard stain for bone, to allow comparison of ossification in fed and unfed larvae.

RESULTS

BEHAVIOR

Newly hatched grunion larvae have functional eyes and jaws and are extremely active (Thompson and Thompson, 1919; David, 1939). Grunion larvae which received food in the present experiment remained very active as they grew, and some schooling behavior was noted as early as day 6. Of more immediate concern was the behavior of starved larvae. On day 7 it was noted that unfed larvae were much easier to catch with a pipette than fed larvae. As the period of starvation lengthened, larval activity declined and the number of larvae remaining quiescent on the bottom increased. Near the end of the experiment, no starved larvae were swimming freely above the bottom, and their activity consisted in occasional erratic movements, followed by long quiescent periods.

SURVIVAL

Figure 1 shows the survival to day 20 of larvae which were fed at various times after

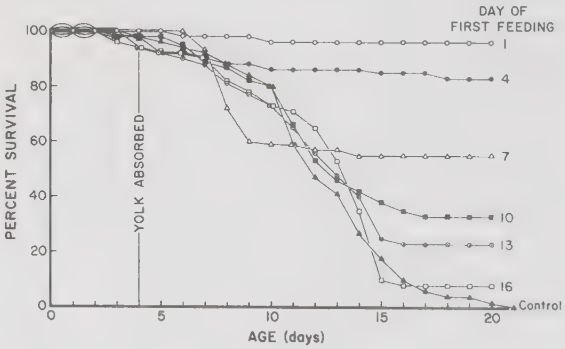

FIGURE 1.—Survival curves for larvae with different times of initial feeding, at 18° C. The number at the end of each curve indicates the day of initial feeding. The control group was given no food during the experiment.

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[4] Hewlett Packard Corporation, Palo Alto, Calif.

hatching and a starved control. Yolk was completely used up in unfed larvae by day 4, and on this day only a minute amount was left in fed larvae. The survival curve for unfed larvae passed the 50% line between days 11 and 12, roughly the same as the starvation time given by Hubbs (1965) for larval grunion at 18° C. The starved control larvae were all dead by day 21. There is a direct relationship between percent survival of original larvae to day 20 and the day of first feeding (Table 1). The number of larvae which survived to day 20, expressed as a percentage of those which were alive when food was first offered, is also listed in Table 1. This figure never dropped below 40%, and all of the previously unfed larvae alive in container #6 on day 16 (i.e., four larvae) began feeding when food was supplied and survived to day 20, and their general appearance and behavior indicated that they would easily have survived longer, had the experiment been prolonged.

TABLE 1.—Survival to day 20 of larvae with different times of initial feeding.

Day of first feeding	Original number of larvae	Number of larvae alive when food first offered	Number of larvae alive on day 20	Percent survival to day 20	
				Original larvae	Larvae alive when food first offered
1	51	51	49	96.1	96.1
4	52	51	43	82.7	84.3
7	53	49	29	54.7	59.2
10	55	44	18	32.7	40.9
13	48	23	11	22.9	47.8
16	51	4	4	7.8	100.0

In the group of larvae which was fed for the first time on day 7, 11 larvae were found dead on the morning following the day of first feeding; 9 dead larvae had food in their guts and 5 of these had guts which were bright orange and so stuffed with *Artemia* nauplii that the abdomen was noticeably distended. In the group fed initially on day 10, all eight larvae found dead the next morning had food in their guts, and four of these had bright orange, packed guts. On day 14, only one out of four dead larvae, found in the container which had been fed for the first time on the previous day, had food in its gut and showed the orange and bulging abdomen noted in dead larvae from the previous two groups.

GROWTH

The increase in length and dry weight of larvae sampled from the "fed" supply containers is presented in Table 2. The rate of growth was higher from day 16 on; variability likewise increased after this time, an example of the "growth depensation" which is commonly found in growing fish (Ricker, 1958). On day 7, the hypural elements were beginning to form along the posterior ventral margin of the notochord, and on day 10 the tip of the notochord was beginning its upward flexion. The greatest increase in length occurred between days 1 and 4, and owing to the upturning notochord the mean length actually decreased between days 13 and 16 (Table 2). On day 4, only the cleithrum and a very few cranial and branchial elements were ossified, but by day 10 about half of the vertebrae (the anterior ones) and some of the caudal rays were beginning to take up alizarin, and by day 16 all vertebrae and hypural elements were ossified.

TABLE 2.—Length and weight of fed and unfed larvae. $\bar{x}$ = mean, *SD* = standard deviation, *n* = number of larvae measured.

Age (days)	Length (mm)						Dry weight (mg)					
	Fed			Unfed			Fed			Unfed		
	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*
1	--	--	--	8.96	0.17	9	--	--	--	0.362	0.021	9
4	9.64	0.34	10	9.31	0.20	10	0.428	0.038	10	0.386	0.030	10
7	10.70	0.59	10	9.27	0.12	10	0.771	0.130	10	0.409	0.015	9
10	11.66	0.28	10	9.11	0.23	10	1.027	0.100	10	0.355	0.032	10
13	12.28	0.34	10	8.98	0.19	10	1.340	0.183	10	0.311	0.013	10
16	12.22	0.60	10	8.78	0.19	10	1.517	0.361	10	0.266	0.018	10
19	13.53	0.58	10	--	--	--	2.433	0.458	10	--	--	--
25	15.12	0.45	10	--	--	--	3.804	0.464	10	--	--	--

Starved larvae exhibited a slow decline in dry weight after yolk absorption, with little variability between larvae (Table 2). Although rudiments of the hypural elements were just discernible in starved larvae on day 7, their notochords never showed evidence of upward flexion, even as late as day 16. On day 16, ossification in starved larvae was comparable to that in fed larvae from day 4 or day 7, with only the cleithrum and a few elements of the cranium and visceral skeleton taking up alizarin.

The lengths and weights of 20-day-old larvae from the delayed feeding series (containers #1-6) are listed in Table 3, and in Figure 2 the weights are plotted and connected by dotted lines to the weights of starved larvae on the days when food was first offered. As expected, the later the initial feeding, the lower the mean weight on day 20, although the range of weights of larvae fed from day 4 falls within that of larvae fed from day 1, and larvae fed from days 13 and 16 likewise overlap (Figure 2). The rate of gain in weight decreases with delay of initial feeding, as indicated by the decreasing slopes of the dotted lines in Figure 2, but these rates are similar to those of larvae feeding for comparable lengths of time from day 1 (e.g., the weight gain of fed larvae between days 1 and 10 is about the same as that of larvae fed initially on day 10 and sampled on day 20). Larvae fed from days 1, 4, and 7 had completed notochordal flexion by day 20, and those fed from day 10 were at an intermediate stage of flexion at this time; in those fed from days 13 and 16, the process of flexion had not yet begun by day 20. Larvae from both the fed series and the delayed-feeding series indicated that notochordal flexion did not begin until a length of about 11 mm and a dry weight of about 1 mg had been reached.

TABLE 3.—Length and weight of 20-day-old larvae with different times of initial feeding. $\bar{x}$ = mean, *SD* = standard deviation, *n* = number of larvae measured.

Day of initial feeding	Length (mm)			Dry weight (mg)		
	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*
1	14.24	0.61	20	2.702	0.420	20
4	14.03	0.36	20	2.513	0.193	20
7	12.38	0.31	20	1.638	0.148	20
10	11.10	0.38	18	0.995	0.086	18
13	9.87	0.51	11	0.561	0.137	11
16	9.82	0.35	4	0.436	0.036	4

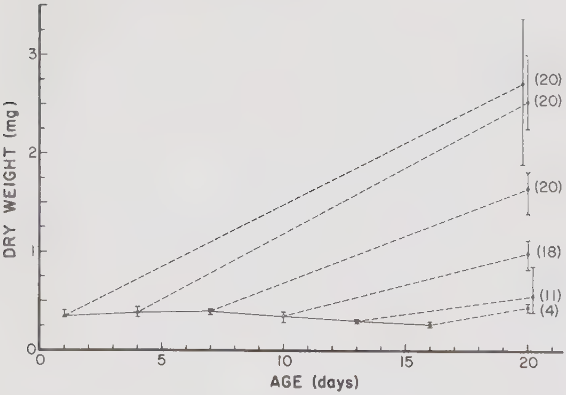

FIGURE 2.—Dry weights of 20-day-old larvae with different times of initial feeding. Means and ranges are plotted, and the number of 20-day-old larvae measured in each group is given in parentheses. Dashed lines connect mean weights at day 20 with the mean weights of unfed larvae on the days when feeding was initiated.

Condition factors have been used in the past to assess the nutritional state of fish larvae (Hempel and Blaxter, 1963; Blaxter, 1965) and were calculated for each sample in the present experiment as

$$\frac{(\text{mean dry weight, mg})}{(\text{mean standard length, mm})} \times 10^3$$

Figure 3A shows that after day 4, the condition factors for fed larvae increased until the end of the experiment on day 25, while those for starved larvae, after showing a slight rise on day 7, decreased until the final sampling on day 16. As shown in Figure 4A, the condition factors of 20-day-old larvae decreased in groups for which initial feeding had been delayed 7 days or more, with larvae fed from day 16 showing a condition factor between those of starved larvae 10 and 13 days old.

FEEDING INCIDENCE

On day 4, larvae which had been offered food since day 1 showed a higher feeding incidence (88%) than those which were given food for the first time on this day (35%)—Table 4. However, on days 7, 10, and 13 the feeding incidence was similar (between 80 and 96%) in larvae which had fed and those which had not fed prior to the test. On day 16, the darkly pigmented abdomen of previously fed larvae made it impossible to determine their feeding incidence, but all of those larvae tested which had received no food prior to day 16 did consume food on this day. The failure of previously fed larvae to show a feeding incidence of 100% in these experiments probably reflects the stress associated with transfer between containers.

TABLE 4.—Feeding incidence of previously fed and unfed larvae. Larvae were exposed to *Artemia* nauplii for 1 hr, after which they were examined for evidence of feeding.

Age (days)	Larvae previously fed			Larvae previously unfed		
	Number of larvae feeding	Number of larvae not feeding	Percent feeding	Number of larvae feeding	Number of larvae not feeding	Percent feeding
4	22	3	88.0	9	17	34.6
7	21	2	91.3	23	1	95.8
10	22	2	91.7	24	1	96.0
13	20	4	83.3	8	2	80.0
16	--	--	--	4	0	100.0

FOOD INTAKE AND CONVERSION

On day 1, the mean dry weight of the larval yolk supply was 0.027 mg (range, 0.015-0.039 mg), and on day 4, fed larvae retained 0.003 mg of yolk (range, 0-0.011 mg) while starved larvae had no yolk left.

In the quantitative feeding experiments, conducted in small, 300-ml containers, some larvae did not survive the 6-day experimental period, and some exhibited erratic swimming behavior. Only data from the surviving larvae which displayed normal behavior have been retained. Larvae did not begin feeding until day 2, although food was available to them on day 1. The number of nauplii consumed daily per larva increased as larvae grew, from less than 50 in first-feeding larvae to almost 300 in larvae 2 weeks old and older. Table 5 gives the total food consumption, growth, and conversion efficiencies of all healthy larvae which survived the feeding experiments in small containers. Larvae which displayed growth comparable to that of larvae in 10-liter containers may be expected to give the most reliable conversion efficiency values and are identified by asterisks in Table 5. One larva, fed from day 1, showed the extremely high efficiency of 73%. Table 5 suggests a trend toward decreasing conversion efficiency as larvae get older. In the experiment begun on day 7, the previously unfed larva for which data are available showed a much higher efficiency than the previously fed larva.

BODY COMPOSITION

Results of the analyses of carbon, hydrogen, nitrogen, and ash in sampled larvae are given

TABLE 5.—Food consumption, growth, and conversion efficiencies of individual larvae in small containers during 6-day feeding experiments. Asterisks identify larvae which exhibited growth comparable to that of larvae in large containers and hence probably provide the most reliable conversion efficiency figures.

Age at start of feeding experiment (days)	Previous treatment	Dry weight (mg)				Percent conversion efficiency [= (gain/total food consumed) × 100]
		Total food consumed	Larva, initial	Larva, final	Larva, gain	
1	--	[1]0.433	0.362	0.678	0.316	73.0*
1	--	[1]0.771	0.362	0.700	0.338	43.8*
4	fed	[2]1.321	0.428	1.189	0.761	57.6*
4	unfed	1.074	0.386	0.880	0.494	46.0
7	fed	1.053	0.771	0.962	0.191	18.1
7	unfed	1.026	0.409	0.826	0.417	40.6
10	fed	2.250	1.027	1.940	0.913	40.6*
10	fed	1.640	1.027	1.528	0.501	30.5*
10	unfed	0.978	0.355	0.668	0.313	32.0
13	fed	2.000	1.340	1.657	0.317	15.9
16	fed	2.365	1.517	2.002	0.485	20.5
		2.155	1.517	2.418	0.901	41.8

[1] Includes 0.027 mg of yolk.
[2] Includes 0.003 mg of yolk.

TABLE 6.—Carbon, hydrogen, nitrogen, and ash in larval samples, as percentages of total dry weight.

Age (days)	Treatment	C (%)	H (%)	N (%)	Ash (%)
1	--	45.7	7.0	10.2	5.1
4	fed	45.5	7.0	10.5	5.4
7	fed	46.2	7.1	10.5	7.9
10	fed	47.1	7.1	10.8	8.6
13	fed	46.2	7.2	11.3	8.6
16	fed	45.2	7.0	10.9	8.7
19	fed	45.0	7.0	10.7	9.2
25	fed	43.1	6.6	10.9	10.0
4	unfed	46.5	6.9	10.4	6.6
7	unfed	44.5	6.9	10.6	7.8
10	unfed	44.0	6.8	11.1	9.4
13	unfed	44.0	6.8	11.2	9.2
16	unfed	43.2	6.4	11.3	7.3
20	fed from day 1	45.0	6.7	11.3	9.9
20	fed from day 4	43.1	6.7	11.1	9.8
20	fed from day 7	44.8	6.8	11.4	9.4
20	fed from day 10	44.8	6.7	10.8	8.2
20	fed from day 13	44.6	6.7	10.9	8.8
20	fed from day 16	43.3	6.5	10.6	11.4

in Table 6. In this paper the term *level* will be used in the sense of Giese (1969) to denote the percentage of the total dry weight which a particular body component constitutes. In fed larvae, the level of ash increased from 5.1% on day 1 to 10.0% on day 25. The ash level was higher in unfed than in fed larvae, except on days 7 and 16. The nitrogen level increased with age in both fed and starved larvae, but the increase was more steady in the latter. Fed larvae fluctuated between 10.7 and 11.3% nitrogen from day 10 to day 25. Accompanying the increase in nitrogen was a decrease in the level of carbon. Among 20-day-old larvae, the level of ash was higher, nitrogen lower, and carbon the same or slightly lower in larvae whose initial feeding had been delayed for 16 days than in larvae fed earlier. Nitrogen in 20-day-old larvae decreased with time of first feeding, from day 7 to day 16. The ratio of carbon to nitrogen has been plotted in Figures 3 and 4 along with condition factors. The C/N ratio is lower in starved than in fed larvae after day 4 but shows a decreasing trend with time even in fed larvae whose condition factor is increasing (Figure 3). On day 20, larvae whose initial feeding had been delayed 10 or more days had higher C/N values than larvae fed earlier; here too, decreasing condition factors accompanied increasing C/N values. Since preservation in Formalin has been shown to affect the C, H, N, and ash levels of copepods

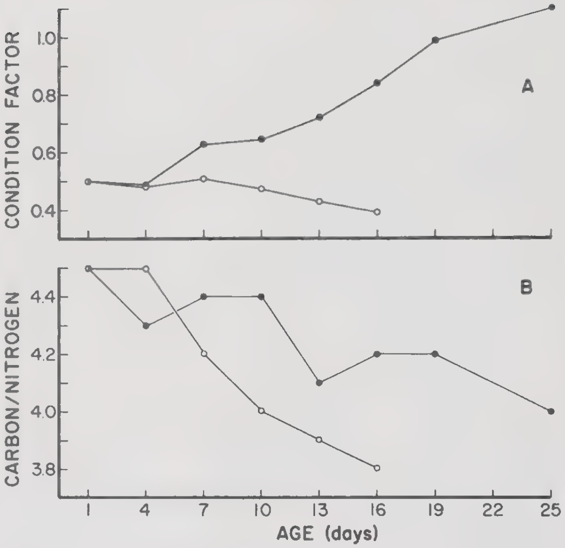

FIGURE 3.—Condition factors and carbon/nitrogen ratios of fed and unfed larvae. Condition factors were calculated as [(mean dry weight, mg)/(mean standard length, mm)] × 10^3. Closed circles = fed larvae, open circles = unfed larvae.

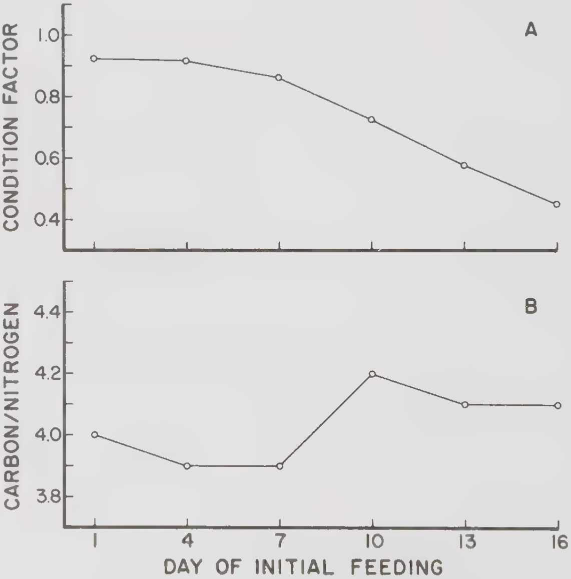

FIGURE 4.—Condition factors and carbon/nitrogen ratios of 20-day-old larvae with different times of initial feeding. Condition factors calculated as in Figure 3.

(Omori, 1970), the values given here for larvae 1 and 4 days old, which had been preserved in Formalin to allow removal of yolk by dissection, may be somewhat in error.

The level of protein in larval samples was estimated by multiplying the nitrogen level by 6.25 (White, Handler, and Smith, 1968), and fat was calculated by difference: 100 - (percent ash + percent protein) = percent fat. Nonprotein nitrogen and carbohydrate were assumed to be present in negligible amounts in this material (Lasker, 1962). Caloric content was calculated by multiplying weights of fat and protein in average larvae by 9.5 cal/mg and 5.7 cal/mg, respectively (Brody, 1945; Kleiber, 1961). Table 7 lists the resulting values. The most notable trends are an increase in protein level and decrease in fat level, in both fed and unfed larvae (Table 7). Unfed larvae had lower fat and about the same or somewhat higher protein levels than fed larvae. Among 20-day-old larvae, those for which initial feeding had been delayed tended to have higher fat and lower protein levels than those fed early (Table 7).

TABLE 7.—Protein, fat, and caloric content of larval samples. Protein and fat are given as percentages of total dry weight. Protein was calculated from the nitrogen content of samples, fat by difference, and caloric content by multiplying weights of protein and fat by standard conversion factors.

Age (days)	Treatment	Protein (%)	Fat (%)	Caloric content	
				cal/mg of dry weight	cal/mg of ash-free dry weight
1	--	63.8	31.1	6.60	6.97
4	fed	65.6	29.0	6.50	6.86
7	fed	65.6	26.5	6.25	6.79
10	fed	67.5	23.9	6.12	6.70
13	fed	70.6	20.8	6.00	6.54
16	fed	68.1	23.2	6.11	6.68
19	fed	66.9	23.9	6.09	6.70
25	fed	68.1	21.9	5.97	6.64
4	unfed	65.0	28.4	6.43	6.89
7	unfed	66.3	25.9	6.26	6.79
10	unfed	69.4	21.2	5.94	6.55
13	unfed	70.0	20.8	5.98	6.60
16	unfed	70.6	22.1	6.13	6.60
20	fed from day 1	70.6	19.5	5.89	6.54
20	fed from day 4	69.4	20.8	5.94	6.59
20	fed from day 7	71.3	19.3	5.90	6.50
20	fed from day 10	67.5	24.3	6.16	6.71
20	fed from day 13	68.1	23.1	6.07	6.65
20	fed from day 16	66.3	22.3	5.89	6.64

Reflecting changes in proximate composition, the caloric content of larval tissue showed an early decrease and from day 10 on showed no increasing or decreasing trend, in both fed and unfed larvae (Table 7). From day 10 on, starved larvae tended to have a lower caloric content than fed larvae. The caloric contents of 20-day-old larvae showed no consistent trend with time of initial feeding (Table 7).

DISCUSSION

The developmental process requires a nutritional input to supply energy and raw materials. In larval grunion which receive no food, development does not progress beyond the stage reached when the yolk is absorbed, although the larvae survive well beyond this point. The process of ossification is halted and the upward flexion of the notochord does not take place in unfed larvae, while tissue resorption, supplying energy for metabolic processes during starvation, results in a slow decrease in larval mass. Fat seems to be utilized most during starvation. The amount of fat in an average starving larva decreases by 0.071 mg, or 0.689 cal, during 16 days of starvation, while protein decreases by only 0.043 mg, or 0.245 cal (Tables 2 and 7). The fat and protein levels of feeding larvae are not greatly different from those of starving larvae (Table 7), but in the former case the observed increase in protein level with time must be a consequence of rapid protein synthesis in the growing organism, whereas in the latter it reflects the utilization of the body's fat reserves.

When food is offered to unfed larvae, growth begins and proceeds at about the same rate as in larvae fed from day 1 (Figure 2). Weight and body composition at day 20 in larvae whose initial feeding was delayed for various periods is close to that of larvae fed for similar lengths of time from day 1 (Tables 2, 3, and 7), though fat is much more depleted in larvae fed for 4 and 7 days starting on days 16 and 13, respectively, than in larvae fed for 4 and 7 days starting on day 1. Larvae fed for a period of 16 days, from day 4 to day 20, gained more weight and had higher protein levels than larvae fed from days 1 to 16 (Tables 2, 3, and 7), suggesting that a few days' delay in initial feeding caused an increase in conversion efficiency. A similar effect has been found in adult fish (Ivlev, 1939; Pandian, 1967). There is some indication in the results of the quantitative feeding experiments that larvae convert food more efficiently after 7 days without food than after 7 days of feeding (Table 5), but the data are too meager to justify any conclusion on this point.

Omori (1970) showed that copepods from areas poor in food tended to have lower C/N ratios than copepods from rich areas. In larval fishes, condition factors have been used in attempts to assess nutritional state (Hempel and Blaxter, 1963; Blaxter, 1965). Both measures were compared in the present study (Figures 3 and 4). Although starved larvae had lower C/N ratios than fed larvae after day 4, due presumably to catabolism of fat, the C/N ratios of growing, fed larvae decreased with age as a consequence of the rapid elaboration of protein, while their condition factors increased. Reflecting this same tendency, larvae 20 days old had higher condition factors but lower C/N ratios, the longer they had been feeding. Condition factor seems to be somewhat more consistent and reliable as an index of the nutritional state of larval grunion than C/N ratio.

In sum, larval grunion appear to be extremely resistant to food deprivation. Under laboratory conditions it takes 3 weeks for all larvae to die of starvation at 18° C (Figure 1). No matter how long initial feeding is delayed, over 40% of the larvae alive when food is offered will survive, and all larvae which survive 16 days without food can commence feeding at this time and survive (Table 1). Since grunion larvae hatch from eggs deposited in the beaches of southern California and northern Baja California and must inhabit inshore waters almost exclusively, and since the abundance of microplankton is extremely high in inshore as compared with offshore waters in this region (Beers and Stewart, 1967), it seems unlikely that these larvae ever experience high rates of mortality due to starvation. Major sources of mortality among grunion larvae must be sought, rather, in predation and physical damage from waves. Tidal variations may result in different incubation periods in grunion eggs from different spawnings (Walker, 1952), but the effect of this on larval viability has yet to be determined.

These findings differ from results for clupeoid larvae. In the northern anchovy a delay in initial feeding of 2.5 days after yolk absorption resulted in nearly complete mortality, even though many larvae were alive when food was administered (Lasker et al., 1970). This "point of irreversible starvation" appears not to exist for larval grunion, as starvation can in fact be reversed at any point along the survival curve of starved larvae (Figure 1).

Larvae of the herring (*Clupea harengus*) show a decrease in the percentage of larvae which commence feeding as the period of food deprivation is lengthened, and the point at which the percentage feeding is half that at the start of the experiment has been termed the "point of no return" (Blaxter and Hempel, 1963; Blaxter, 1965). Again, the grunion larvae show a different pattern, with at least 80% of the larvae commencing feeding when food is offered after periods of starvation ranging from 7 to 16 days (Table 4). Some larvae which did commence feeding after 7, 10, and 13 days without food were nevertheless unable to survive and died after gorging themselves with *Artemia* nauplii. The interesting fact that all of the larvae alive after 16 days of starvation commenced feeding and survived, while the percentage feeding was lower in larvae starved for shorter periods of time, may be explained as a result of mortality among the weakest larvae, so that by day 16 only the most hardy individuals were still alive.

Thus, certain types of larvae would be more likely than others to show a "critical period" pattern of mortality at sea under conditions of low food availability. If northern anchovy larvae were not to encounter food within 2.5 days after yolk absorption, there would ensue a catastrophic mortality concentrated in time (Lasker et al., 1970). In contrast, grunion larvae, which hatch in a more well-developed and robust state, would exhibit mortality extending over a number of days if deprived of food and hence would not show a "critical period" in the classical sense of Hjort. Obviously a sudden increase in mortality at sea could come about after yolk absorption, or at any other time, owing to factors other than the availability of food. Hjort was, of course, not referring to larvae of the atherinid type when he enunciated his "critical period" hypothesis, but with the large volume of published material now available concerning the larvae of a few commercially important species, it would be easy to lose sight of the great diversity of larval forms and to apply ideas which may have validity in some groups to groups in which they have no place.

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7137

VARIABILITY OF NEAR-SURFACE ZOOPLANKTON OFF SOUTHERN CALIFORNIA, AS SHOWN BY TOWED-PUMP SAMPLING

CHARLES P. O'CONNELL[1]

ABSTRACT

Variations in the density of near-surface populations of small copepods, large copepods, euphausiids, and chaetognaths are described for an area of 6,000 square miles off the coast of southern California from three cruises in the autumn of 1961 and two cruises in the autumn of 1962. Samples were collected with a towed pump at a depth of 5 m. Approximately 162 samples, each representing a 1-mile transect, were collected on each cruise.

Median densities for the cruises showed some significant differences for each species group. The frequency distribution of densities within the area on individual cruises varied from positive skewness at low general levels to relative symmetry at high general levels for the three crustacean groups, but was skewed at all levels for chaetognaths. Within sampling blocks of 20 square miles, the range of density varied with the median as $\log R = 0.35 + 0.8 \log M$. Range is greater than the median when the latter is less than 50, but less than the median when it is higher than 50.

Euphausiids and large copepods showed greater diurnal change than small copepods and chaetognaths.

Dry weight concentration of samples, averaged over all cruises, was 17.3 mg/m^3 for the day period (0600-1800) and 25.1 mg/m^3 for the night period. Most of the nighttime increase is attributable to the euphausiid group.

The three crustacean groups, and dry weight, showed significant inverse trends with temperature, but not with distance from land. The trends with temperature reflect events in 1961 but not in 1962.

These variations suggest that food potential of plankton for pelagic fishes may be appreciably greater than indicated by general averages for the area, depending on the degree of selectivity and orientation to small-scale features of distribution by the fishes.

Little is known about the effects of plankton variability on the distribution, movements, or rate of feeding of pelagic fishes which feed on plankton. It has been demonstrated experimentally (Ivlev, 1961) for some fishes that rate of feeding varies not only with average density but also with the degree of aggregation of food organisms in an area. Plankton density is known to vary diurnally (Cushing, 1951; King and Hida, 1954) as well as seasonally and annually, and there is evidence of aggregation in the variation for both small and broad spatial scales (Barnes and Marshall, 1951; Cassie, 1959, 1962, 1963). The plankton pump surveys reported here were undertaken to obtain information on variability and trends in variability for four plankton species groups commonly present in near-surface waters along the southern California coast. Though surveys were limited to the autumn seasons of 2 consecutive years, the data should be a useful guide in evaluating the food potential of near-surface plankton distributions in the region.

COLLECTION OF SAMPLES

Samples were collected with the towed pump and shipboard filtering system described by O'Connell and Leong (1963). The 1.9-cm (¾-inch) orifice of the pump pointed forward to achieve a coring orientation, and the rate of pumping (98 liters/min) exceeded the passive coring rate to produce in effect a 5.8-cm (2-inch) diameter coring cross-section. Operation of the system was essentially a matter of leaving the pump in tow and running throughout a cruise pattern with the incoming water stream diverted to the scuppers except while traversing sampling blocks, at which time the flow was directed through the filtering apparatus. The stainless steel filtering screen (105μ mesh) retained

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virtually all organisms as small as 200μ in length (O'Connell and Leong, 1963) or 100μ in diameter (Leong, 1967). The upper size limit was less easily defined, but organisms as long as 14 mm were delivered at the filtering apparatus, though the large individuals were often mutilated.

Five cruises were carried out, three in September to November 1961 and two in the same period of 1962. For each cruise a pattern of 18 sampling blocks was selected from a possible 281 that covered an area of almost 6,000 square miles (Figure 1). To insure reasonably good coverage of the entire area, the population of blocks was divided into three approximately equal subareas and a set of six blocks was selected at random from each. The blocks were occupied by the shortest practical track from northwest to southeast. Each cruise pattern required about 2.5 days of vessel time.

Each sampling block was 51.8 km^2 (20 square miles) in area, the only exceptions being some of the blocks adjacent to the coast or to islands. Nine 1.6-km (1-mile) samples were collected at each block in a continuous series along two connecting sides (Figure 1, insert) and were preserved in Formalin for laboratory processing.

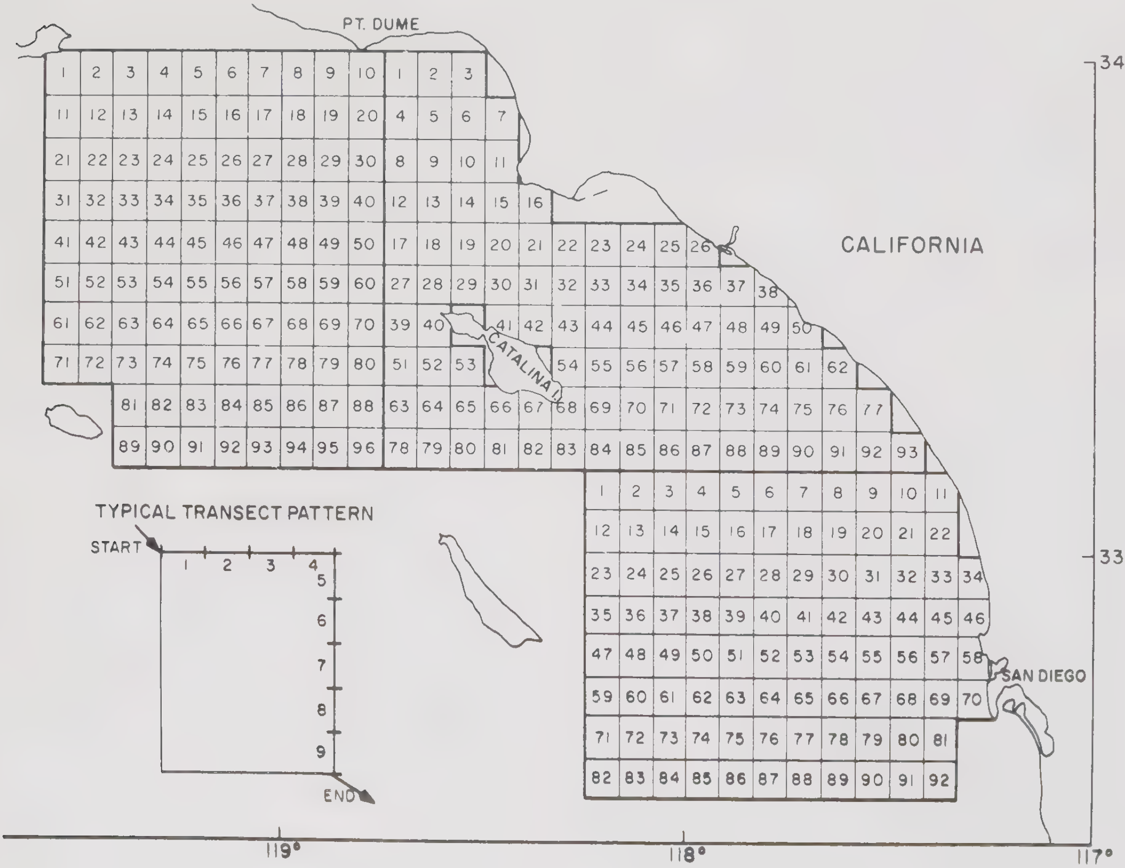

FIGURE 1.—The sampling area and entire population of sampling blocks. Six blocks were randomly selected from each of the three subareas for each cruise and occupied by the shortest route from north to south. Sampling blocks are 4 × 5 miles and the insert shows the manner of transect sampling. Four of the nine samples from each block were selected randomly for organism enumeration.

Consecutive 1.6-km samples were separated by shifting the incoming stream to a new filter every 6.5 min. Water volume, recorded for each sample from a meter in the incoming line, averaged 636.7 liters (standard deviation 47.8). Water temperature of the incoming stream was recorded at approximately the midpoint of each series of block samples. Continuous thermograph records indicated that surface water temperature did not change appreciably during the sampling of individual blocks.

SAMPLE PROCESSING

Four of the nine samples from each block were randomly selected for the estimation of numbers of organisms. Of the remaining five, one was chosen at random to be reserved for special purposes such as length and dry weight measurements of species groups, and the other four were pooled to obtain a dry weight value for the block. Estimates were standardized as quantities per m^3 on the basis of the actual volumes of water filtered in the samples.

Estimates for two size categories of copepods, 0.2 to 0.9 mm in length and all over 1.0 mm long, and for euphausiids and chaetognaths, were made by volumetric subsampling with replacement, i.e., each subsample was returned to the sample before the next subsample was drawn. The volumetric subsampling technique yields estimates of satisfactory precision only if organisms are randomly distributed in the sample container prior to the removal of each subsample. Simple stirring accomplished this for all species groups except the small copepods, probably because they were entangled in phytoplankton present in the samples. Random distribution was assumed to exist where the value s^2/x did not exceed $\chi^2/N\text{-}1$ for a series of subsamples (Holmes and Widrig, 1956). A random distribution was achieved for the small copepods by subjecting the sample to a few 1-sec bursts of rapid stirring in a Waring Blender.[2] However, because this treatment fragmented some larger organisms a two-step procedure was employed: all organisms except the small copepods were estimated by subsampling following gentle stirring; the sample was then agitated in the Waring Blender, after which the small copepods were estimated by subsampling.

Estimates for the small copepods were always based on subsample counts totaling 200 to 300 from the sample. With the assumption of random distribution, the number in the sample should in all cases be within 15% of the estimate for $p = 0.05$ (Holmes and Widrig, 1956). More than half of the sample estimates for the other three species groups were based on counts of 30 or more, for which the number in the sample should have been within 40% of the estimate. For the remainder, where numbers counted were low, examination was not extended beyond subsamples totaling one-third the volume of the sample container, 2,000 ml.

In addition to the four species groups counted, the samples contained larvaceans and small invertebrate eggs (0.15-0.35 mm diameter), sometimes in moderately high numbers. Larvacean tails and heads were separated, however, and invertebrate eggs were not readily distinguishable from the latter. Cladocerans and polychaetes were generally absent or low in number, though each occurred in high numbers in a few samples. Fish eggs occurred rarely and in low numbers.

SIZE OF ORGANISMS

Length measurements for 10 day samples (0600-1800) and 10 night samples are summarized in Table 1 and Figure 2. Measurements were total length except for euphausiids, which were measured from the carapace behind the eye to the junction of the abdomen and telson. Data from day and night samples were pooled for small copepods and chaetognaths but not for large copepods and euphausiids, which showed appreciable size frequency differences for the two periods.

The length-frequency distribution for the small copepod group, composed largely of naupliar and copepodite stages, is nearly symmetrical, with the mean and the median close to the midpoint of the predetermined size range (0.20-0.99 mm long). Almost one-third of the organisms

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[2] The use of trade names is merely to facilitate descriptions; no endorsement is implied.

TABLE 1.—Length data for species groups.

	Mean length	Median length	Minimum length	Maximum length
	mm	*mm*	*mm*	*mm*
Small copepods	0.58	0.56	0.20	0.99
Large copepods:				
Day	1.94	1.90	1.00	5.30
Night	1.75	1.61	1.00	4.20
Euphausiids:				
Day	2.3	2.1	0.6	9.7
Night	5.7	5.9	1.1	10.6
Chaetognaths	6.4	5.5	2.0	14.5

were between 0.5 and 0.6 mm in length. It is possible that the decline in numbers below the median length was partly the result of increasing escapement with diminishing size, but the escaping fraction, known to be negligible for sizes above 0.4 mm, is assumed to be relatively small for sizes down to 0.2 mm (O'Connell and Leong, 1963). On this assumption the length-frequency distribution is considered representative for this size range of copepods.

The large-copepod group shows a modal shift to smaller sizes at night, although the size range and degree of skewness are not markedly different for the two periods. Organisms less than 1.5 mm in length were largely copepodites, while those between 1.5 and 3.0 mm were adult *Calanus helgolandicus* and *Paracalanus* sp., with *Centropages* sp. also present in the night samples. Those larger than 3.0 mm were largely *Rhincalanus* sp. in both day and night samples.

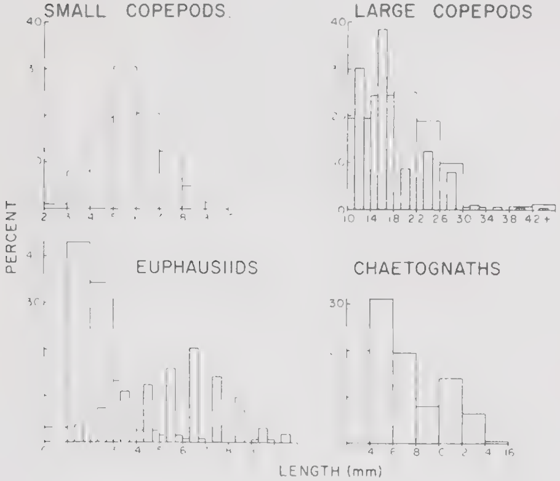

FIGURE 2.—Length-frequency histograms of organisms in four species groups, as determined from selected samples. For large copepods and euphausiids the wide bars show day frequencies and the narrow bars night frequencies.

The euphausiid group, which appeared to be composed largely of *Euphausia pacifica*, though *Nyctiphanes simplex* and *Nematoscelis difficilis* were also in evidence, showed a marked shift to larger sizes at night, obviously the result of vertical migration. It is apparent from the sizes involved that the day samples were composed mostly of larval stages and the night samples of larval stages and juveniles, with few if any adults. The largest individuals in the samples were considerably smaller than the maximum total length for the species, 25 mm (Boden, Johnson, and Brinton, 1955).

The pump samples did show some evidence of fragmentation of larger euphausiids, and for this reason the size frequency distribution for the night period might be slightly biased in favor of the smaller sizes, and estimates of numbers sampled might be a little low.

Fragmentation probably involved far more juveniles than adults. Samples from opening-closing nets 1 m in mouth diameter taken in spring and summer off southern California (Brinton, 1962) showed adults to be scarce or absent in the upper 10 m during the night as well as the day. Juveniles were predominant at this stratum. Even at depths where adults were most abundant at night—40 m in one case and 140 to 280 m in another—they were only one-fifth and one-tenth as numerous as juveniles. Nighttime oblique hauls with nets 1 m in mouth diameter off central Baja California indicated essentially the same kind of vertical distribution for euphausiid species in that area (Ahlstrom and Thrailkill, 1963). On the basis of such evidence it seems probable that the size-frequency distributions shown by the pump samples are reasonably representative of the day and night populations near the surface, though certainly not of the population in the entire water column.

The chaetognath group was composed largely, if not entirely, of *Sagitta euneritica*, and the size range is probably representative for the near-surface population sampled. The size range for the species is 1.0 to 15.5 mm in length (Alverino, 1961), and the samples contained individuals from 2.0 to 14.5 mm long.

VARIATION BETWEEN CRUISES

Table 2 shows characteristics of the frequency distributions of all 1.6-km samples by cruise and period of the day for the four species groups. Median densities are lower than mean densities in every instance but one, the nighttime period for small copepods on cruise 5, indicating that distributions for virtually all arrays show some degree of positive skewness. Differences between cruises are described in terms of the medians to avoid undue effects of extreme values that can arise in moment measures on nonnormal populations.

Nighttime median densities are higher than daytime medians on all cruises for small copepods and euphausiids, and on all but the fifth cruise for large copepods. However, variation was such that day and night medians differed significantly ($p<0.05$, Tate and Clelland, 1957) in only one instance for small copepods, three instances for large copepods, and two instances for euphausiids. Though none of these groups can be considered to show consistently higher densities at night for the area as a whole, real differences occurred more often for the large copepods and euphausiids than for the small copepods. Day and night median densities for chaetognaths do not differ significantly for any of the cruises.

Daytime median densities do not differ significantly between cruises for chaetognaths or euphausiids, but those for small copepods and large copepods differ significantly ($p<0.05$) for about half the comparisons. Nighttime medians (Figure 3) show a pattern similar to the daytime sets for the two copepod groups but show, in addition, a number of significant differences between cruises for the euphausiids and one difference for chaetognaths. Median densities of the small copepods were significantly higher for

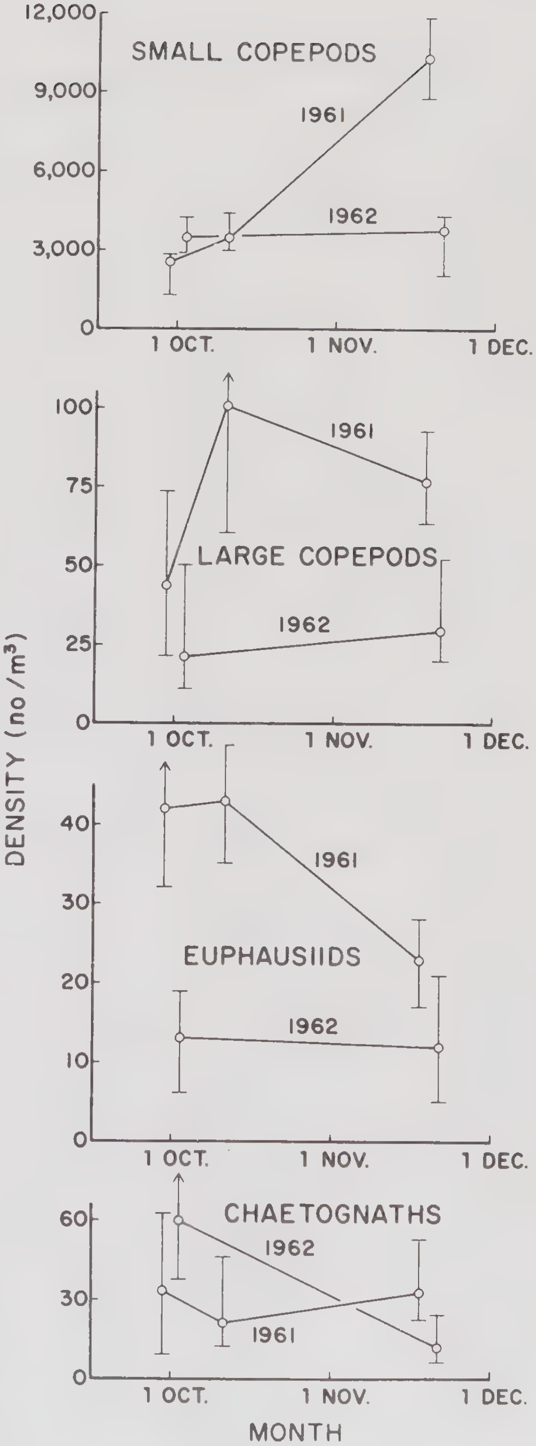

FIGURE 3.—The nighttime cruise medians for four species groups shown by cruise date. Vertical bars indicate the 95% confidence intervals.

TABLE 2.—Summary of density estimates (no/m^3) of 1.6-km samples by cruise, constituent group, and period of day.

	Mean	s	Median	Confidence limits[1] p = 0.95		Minimum	Maximum
				Lower	Upper		
			Cruise 1, September 26-28, 1961, N = 32 day, 40 night				
Small copepods:							
Day	2,569.7	987.4	2,275.5	2,023	2,552	1,210	5,233
Night	2,983.9	1,356.2	2,542.0	2,252	2,792	1,075	7,103
Large copepods:							
Day	6.4	16.0	1.0	0	5	0	83
Night	72.8	95.5	42.5	22	73	0	500
Euphausiids:							
Day	6.7	9.4	3.0	2	8	0	38
Night	52.2	37.1	41.5	32	57	10	172
Chaetognaths:							
Day	84.2	122.9	21.0	8	105	2	488
Night	123.6	244.2	33.0	10	63	2	1,153
			Cruise 2, October 9-11, 1961, N = 24 day, 40 night				
Small copepods:							
Day	3,379.0	1,773.1	3,034.5	2,217	3,527	1,550	7,532
Night	3,953.0	1,620.0	3,325.0	2,942	4,257	2,142	8,118
Large copepods:							
Day	47.3	104.5	1.0	0	17	0	440
Night	102.7	67.3	101.0	60	128	5	250
Euphausiids:							
Day	10.9	19.7	1.0	0	15	0	88
Night	48.2	31.7	42.5	35	50	7	145
Chaetognaths:							
Day	132.7	135.3	121.5	3	198	0	420
Night	51.8	61.9	21.0	13	47	2	280
			Cruise 3, November 16-18, 1961, N = 28 day, 40 night				
Small copepods:							
Day	8,679.0	3,969.7	7,381.5	6,107	10,208	3,752	19,868
Night	10,577.8	3,060.7	10,281.0	8,673	11,812	4,948	17,568
Large copepods:							
Day	18.3	21.1	10.0	5	18	0	92
Night	83.0	42.9	77.0	63	95	10	183
Euphausiids:							
Day	15.5	13.9	13.0	5	22	0	48
Night	39.5	50.8	23.0	17	28	2	243
Chaetognaths:							
Day	73.5	104.5	36.0	32	42	12	470
Night	44.5	38.8	32.5	23	50	3	188
			Cruise 4, October 1-3, 1962, N = 43 day, 26 night				
Small copepods							
Day	2,718.1	1,748.8	1,993.0	1,739	2,771	456	8,190
Night	3,524.1	1,087.1	3,504.0	2,854	4,179	1,477	5,560
Large copepods:							
Day	21.3	19.6	18.0	10	22	0	90
Night	33.6	29.5	21.5	11	50	3	99
Euphausiids:							
Day	8.2	9.1	4.0	3	10	0	39
Night	16.0	14.3	13.0	6	19	1	58
Chaetognaths:							
Day	116.7	164.6	57.0	35	133	9	993
Night	86.9	71.6	60.0	38	113	13	257
			Cruise 5, November 19-21, 1962, N = 32 day, 31 night				
Small copepods:							
Day	3,728.2	2,277.8	3,487.0	2,235	4,328	1,654	11,613
Night	3,505.3	1,962.1	3,750.0	2,054	4,223	796	9,476
Large copepods:							
Day	121.5	252.0	49.5	29	70	0	1,220
Night	41.1	35.6	30.0	19	52	1	154
Euphausiids:							
Day	9.8	11.0	6.5	1	13	0	48
Night	24.4	34.4	12.0	5	21	0	163
Chaetognaths:							
Day	32.2	20.8	28.5	19	41	3	94
Night	21.0	20.2	12.0	7	25	0	72

[1] Confidence limits are for medians (Tate and Clelland, 1957).

each successive cruise in 1961, and the median for the last cruise in this year was more than three times as high as any of the others. Median densities of the large copepods were two to four times as high for the last two cruises in 1961 as for the other cruises. Euphausiid medians were about twice as high for the first two cruises of 1961 than for the other cruises. The chaetognath median for the last cruise of 1962 was significantly lower than for the first cruise of that year, but no other differences can be distinguished.

In summary, the three crustacean groups showed real differences in density near the surface at night for the area as a whole. All showed differences of three to four times between the 2 successive years. The euphausiids and small copepods also showed real differences of about two and three times within the first of the 2 years.

VARIATION WITHIN THE AREA

The 1.6-km samples were taken in block clusters so that small-scale variability could be described in respect to variability over the entire area. The possibilities of comparison are limited, however, because parametric analyses were avoided. The necessary assumptions about frequency distribution of sample estimates could not be satisfied for the present data. Frequency distribution of block medians (or means) is variable between cruises.

FREQUENCY DISTRIBUTION OF BLOCK MEDIANS

Table 3 shows the frequency distribution of block medians for the day and night periods of each cruise. The distributions for each species group vary noticeably, but there are similarities

TABLE 3.—Frequency distribution of block medians by cruise and day (D) or night (N) period.

Class (*no/m*^{3})	1D	1N	2D	2N	3D	3N	4D	4N	5D	5N
Small copepods:										
1-3,000	6	7	3	4	--	--	8	3	4	4
3,001-6,000	2	3	2	5	--	--	3	4	4	5
6,001-9,000	--	--	1	1	5	4	--	--	--	--
9,001-12,000	--	--	--	--	1	2	--	--	1	--
12,000-15,000	--	--	--	--	1	4	--	--	--	--
Category	1	1	2	2	3	4	1	2	2	2
Large copepods:										
0	3	--	3	--	--	--	--	--	--	--
1-50	5	5	2	3	7	1	11	5	6	7
51-100	--	3	--	2	--	7	--	2	1	1
101-150	--	1	--	3	--	2	--	--	--	1
151-200	--	--	--	2	--	--	--	--	1	--
201+	--	1	1	--	--	--	--	--	1	--
Category	1	3	1	4	1	4	1	2	3	2
Euphausiids:										
0	2	--	2	--	1	--	2	--	1	--
1-25	5	2	3	2	5	5	9	6	8	7
26-50	1	3	1	4	1	3	--	1	--	1
51-75	--	3	--	3	--	1	--	--	--	--
76-100	--	2	--	1	--	--	--	--	--	1
101-125	--	--	--	--	--	--	--	--	--	--
126-150	--	--	--	--	--	--	--	--	--	--
151+	--	--	--	--	--	1	--	--	--	--
Category	1	3	1	3	1	2	1	2	1	2
Chaetognaths:										
1-50	5	6	2	7	5	7	4	2	8	9
51-100	1	2	1	1	1	2	3	2	1	--
101-150	--	--	--	1	1	1	3	2	--	--
151-200	--	--	2	1	--	--	--	--	--	--
201-250	1	1	--	--	--	--	--	1	--	--
251-300	1	--	1	--	--	--	--	--	--	--
300+	--	1	--	--	--	--	1	--	--	--
Category	1	1	3	2	2	2	3	3	2	2

among them suggestive of trends with the general level of density. To define the trends, the distributions for each species group were pooled into three or four categories on the basis of the extent of concentration in specific frequency classes and the extent of dispersion over all classes. Category designations are indicated in the table, and percentage frequency histograms are shown for each category in Figure 4. Number of blocks, number of night and day periods, and the range of cruise medians (from Table 2) are given for each histogram.

The histograms suggest the same kind of trend for the three crustacean groups: a shift from distribution almost entirely restricted to the lowest classes when general area level is low, through distribution of greater positive skewness for intermediate levels of area density, to symmetrical distribution as blocks of low median value disappear at the higher levels of area density. The chaetognath distributions were more difficult to classify, but it appears that frequency distribution is appreciably skewed at all levels of area density for this group.

The differences in the trends for the four species groups are also illustrated by the extent of the overlap between the distributions for the highest and lowest categories in the figures. There is no overlap for small copepods, perhaps 50 to 75% overlap for large copepods and euphausiids, and complete overlap for chaetognaths. These differences suggest that when the overall area median is at one extreme, the possibility of blocks with medians at the other extreme is greatest for the chaetognaths, least for the small copepods, and intermediate for the large copepods and euphausiids.

The existence of such trends in frequency distribution indicates that, at least for the crustaceans, no one statistical distribution would satisfactorily fit all the data sets; nor would any single normalizing transformation be uniformly effective for the different data sets. Without normalized distributions, even the interpretation of coefficients of variation would be difficult in comparing cruise periods. It may be noted, however, that when all frequency distribution categories are pooled, the distributions for the four species groups show similar degrees of skewness. The total block array for each species group is approximately normalized by log transformation.

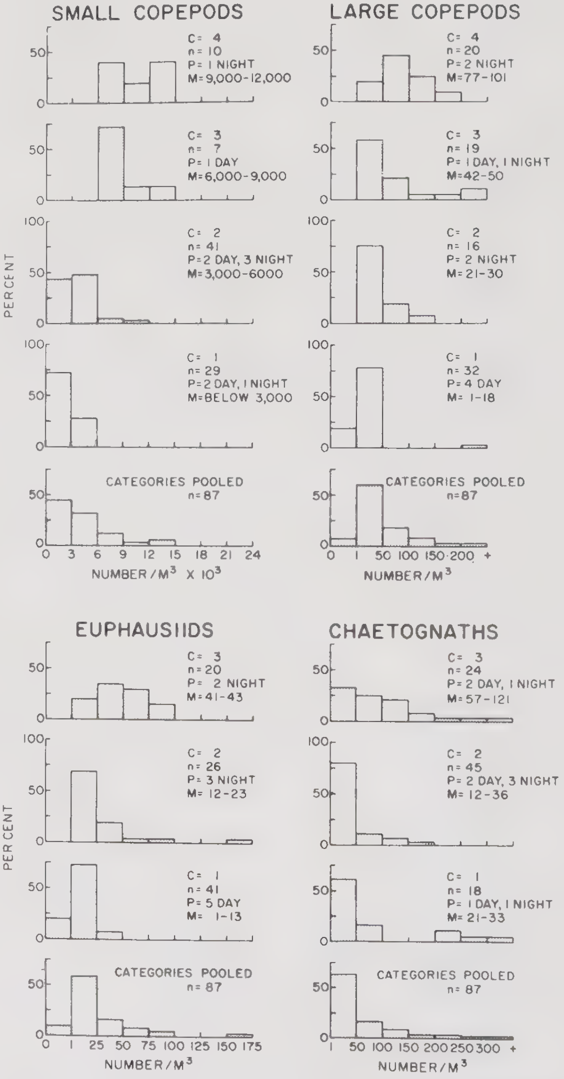

FIGURE 4.—Percent frequency distribution histograms for four species groups as pooled on the basis of similarity. Range of sample medians (M) (from Table 2), number of day and night periods (P), and number of sampling blocks (n) represented by each histogram category (C) is shown. The histogram at the bottom of each set shows the distribution of all block medians from all cruises.

RELATION OF RANGE TO MEDIAN IN SAMPLING BLOCKS

Within block variation is indicated for each species group and for all species groups together by regression $\log R = a + b \log M$ (Table 4), where R = block range and M = block median. The slopes, b, for the five equations do not differ significantly from each other ($p = 0.05$). All are significantly greater than 0 ($p = 0.01$), and all but that for small copepods are significantly less than 1.0 ($p = 0.05$). The intercepts are all significantly greater than 0, again except for the small copepods, but they do not differ significantly from each other ($p = 0.05$). In view of the similarities, the regression for all groups combined (Figure 5) is a satisfactory description of the average relation of block range to block median for each of the species groups.

TABLE 4.—Estimated coefficients for regressions of log block range on log block median for each species group and all species groups combined.[1]

Species group	N	a	b	s	r
Small copepods	87	—.18	.95**	.40	.53**
Large copepods	81	.51	.72**	.36	.74**
Euphausiids	79	.38	.72**	.30	.79**
Chaetognaths	86	.26	.87**	.33	.82**
Combined	333	.35	.80**	.35	.93**

[1] N = number of sampling blocks; a = intercept; b = slope; s = standard deviation about the line; r = correlation coefficient.
** $p = 0.01$.

The regression for all groups combined indicates that average block range increases with block median but not proportionately. The expected ranges for different medians are:

Median	1	10	50	100	1,000	10,000
Range	2	14	51	89	562	3,548

Thus range will tend to be greater than the median when the latter is below 50, but appreciably less than the median when the median is above 100. Small copepods are the only group with consistently high medians, and they also have the greatest standard deviation about the line. This suggests that, while the ratio of range to median is lower, on the average, for this group, it also tends to be more variable than for the other groups.

The relation of block range to the total variation within the area is suggested by the magnitude of block ranges relative to the class intervals of the frequency distributions shown earlier (Table 5). In the case of small copepods, block ranges only slightly exceed the size of class intervals for the two highest classes in the distribution. For the other three species groups, block ranges exceed the class intervals for all but the lowest class. Ranges tend to be spread over three or more class intervals for the upper halves of the euphausiid and chaetognath distributions. Even though the highest classes tend to be rare, it can be seen that ranges extending over two or more class intervals would not be uncommon for large copepods, euphausiids, and chaetognaths.

TABLE 5.—The number of class intervals encompassed by the range for the midpoint of each class interval in the frequency distribution for each species group. The 0-1 class is excluded and other classes are numbered consecutively.

Frequency class	Small copepods	Large copepods	Euphausiids	Chaetognaths
1	0.1	0.6	0.7	0.6
2	0.3	1.4	1.6	1.4
3	0.9	2.1	2.4	2.1
4	1.2	2.8	3.2	2.8
5	1.5	3.4	3.9	3.4
6	--	--	4.6	4.0
7	--	--	5.2	4.6

DIURNAL VARIATION

It is evident from the differences in day and night sets of data that density level near the surface is influenced by diurnal vertical movements, particularly for the larger crustacean groups. The pattern of change is indicated for each of the species groups by medians for 4-hr time intervals (Figure 6). A sequence of change is most apparent for the large copepods and euphausiids, the lowest medians occurring between 1000 and 1400 hr and the highest between 1800 and 0200 hr. The increase in the evening appears to be more rapid than the decrease in the morning for both groups.

The small copepods show a pattern similar to that for large copepods, but much weaker. The highest time interval median is almost 10 times the lowest for large copepods but less than 2 times the lowest for small copepods.

Chaetognaths show only slight evidence of diurnal change. The peak between 0600 and

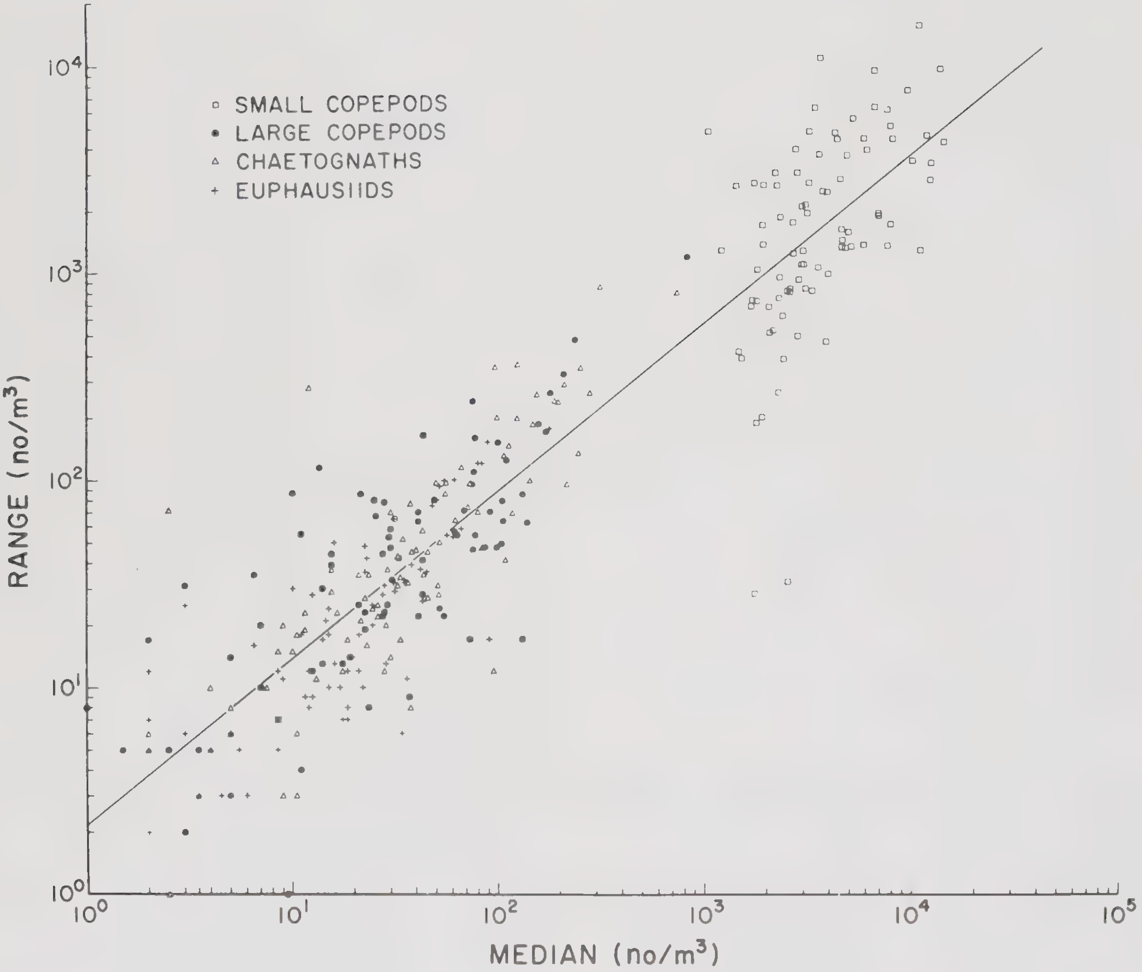

FIGURE 5.—The relation of sampling block range to sampling block median for the four species groups combined.

1000, which is obviously responsible for the generally higher day-period densities shown elsewhere, may indicate an upward and a downward movement in the morning.

The spread of block medians tended to be associated with the time-interval medians for euphausiids but not for the other species groups. The euphausiids showed both high and low block medians at night but only low medians during the middle of the day. Large copepods showed a similar distribution except that three of the highest four block medians in the series occurred between 1000 and 1800 hr. Small copepods and chaetognaths showed high and low medians in all time periods.

CORRELATIONS BETWEEN DENSITIES OF THE FOUR SPECIES GROUPS

The data were examined for association between the densities of species groups over the area by calculating rank-difference correlation coefficients (Tate and Clelland, 1957) for the nighttime block medians of each cruise (Table 6). Daytime blocks were excluded to reduce the component of correlation that would result from

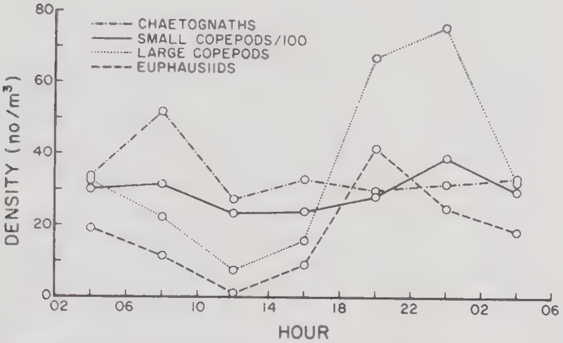

FIGURE 6.—The relation of median density to time of day for four species groups. The points are medians for block densities in 4-hr intervals. The small copepod medians were divided by 100 to put them on the same scale as the others.

TABLE 6.—Rank difference correlation coefficients for median block densities of four species groups for the night periods of five cruises.

	Cruise				
	1	2	3	4	5
Small copepods : large copepods	—.45	.31	.25	.71	.20
Small copepods : euphausiids	—.09	—.20	.59*	.14	.87**
Small copepods : chaetognaths	.26	—.36	—.43	—.42	.30
Large copepods : euphausiids	.10	.04	.71*	.14	.29
Large copepods : chaetognaths	.02	.29	.20	.21	.73*
Euphausiids : chaetognaths	.42	.12	—.23	.00	.53
Number of night blocks	10	10	10	7	9

* $p = 0.05$.
** $p = 0.01$.

the parallel patterns of diurnal change in the crustacean groups.

The coefficients for each of the six species group combinations varied widely among the five cruises, with only four of the entire 30 coefficients indicating significant correlations. It appears that, while occasional correlations can be expected to occur over the area, consistent trends of association in density do not occur among these four species groups near the surface at night.

DRY WEIGHT VARIATION

Dry weight concentrations are summarized by cruise period in Table 7 and by weight class for all cruises in Figure 7. Low and high values occur both night and day, but there is clearly a shift to higher values at night.

The sample concentrations may underestimate the true concentrations by as much as 15 or 20%. Ahlstrom and Thrailkill (1963) showed that for copepods dry weight decreased about 15% after Formalin preservation. Lasker (1966) showed that dry weight of euphausiids was about 35%

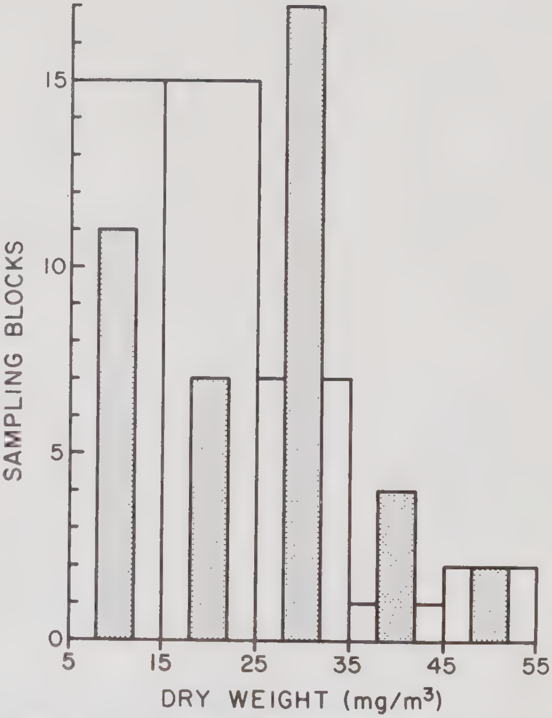

FIGURE 7.—Dry weight frequency distribution of all sampling blocks. The wide bars show day frequencies and the narrow bars night frequencies.

TABLE 7.—Summary of sample dry weight concentration (mg/m³) by cruise and day (D) or night (N) period.

	1D	1N	2D	2N	3D	3N	4D	4N	5D	5N
Mean	13.04	20.87	18.02	22.24	22.94	34.01	22.67	24.51	18.44	25.58
Median	15.00	18.32	14.51	21.03	22.76	31.80	15.24	24.72	15.27	23.23
Minimum	5.81	9.36	5.54	13.54	14.17	25.79	7.02	9.68	8.46	9.54
Maximum	20.85	34.00	43.74	30.57	30.42	49.59	56.90	34.62	32.11	52.42
Number blocks	7	9	6	7	7	9	11	7	9	9

lower for preserved than for fresh material. These groups were prominent in the pump samples, and dry weight determinations were made after long Formalin preservation. The pump samples undoubtedly contained a higher proportion of small copepod forms than the net samples of Ahlstrom and Thrailkill (1963), and it is possible that dry weight loss in Formalin is less for the smaller than for the larger individuals of this group.

As a basis for estimating the contributions of different species groups to dry weight concentration, dry weight factors were determined for large copepods, euphausiids, and chaetognaths by sorting known numbers of each from a few representative samples for drying and weighing. The resulting values are given in Table 8. The factor given for small copepods, which would have been difficult to separate in sufficient numbers and purity for a direct determination, was inferred from data given by Marshall and Orr (1955) for *Calanus finmarchicus* and *C. helgolandicus* in eastern Atlantic waters. They showed that *Calanus* stage V, at an average length of 2.5 mm, have a dry weight of about 300 mg/1000 organisms, and that according to Bogorov (1933) one stage V organism is equal in dry weight to two stage IV, 11 stage III, 42 stage II, and 60 stage I organisms. The average lengths of these stages are given as 2.1 mm, 1.65 mm, and 0.94 mm, and the average length of nauplii is given as 0.585 mm, which is the same as that of small copepods in the present study. Large copepods from the present study show an average length intermediate between those given for stages IV and III above, suggesting a ratio of six large copepods to one stage V, or a dry weight of 50 mg/1000 organisms, which is very close to the actual determinations. No dry weight equivalent is given by Bogorov for nauplii, but extrapolation of his series against average lengths suggests that 120 nauplii per stage V *Calanus*, or 2.5 mg/1000 nauplii, would be a conservative estimate.

TABLE 8.—Dry weight (DW) and ash weight (AW) determinations (mg/1000 organisms) for species groups in selected samples.

	DW	AW	AW/DW
	mg/1000	*mg/1000*	*%*
Small copepods	[1]2.5	--	--
Large copepods:			
Day	54.64	3.48	6.36
Night	49.88	2.94	5.89
Euphausiids:			
Day	42.03	3.29	7.82
Night	293.26	14.51	4.95
Chaetognaths	23.5	1.30	5.51

[1] Not determined by direct measurement. See text.

Dry weight concentrations were calculated for each species group in each block from the dry weight factors and from the medians of numerical estimates for the blocks. The values for species groups were summed to produce a "calculated" dry weight concentration for each block. These are compared to the measured dry weight concentrations in Figure 8. All the data together tend to cluster around the line of equal value (slope 1.0), and each of the different

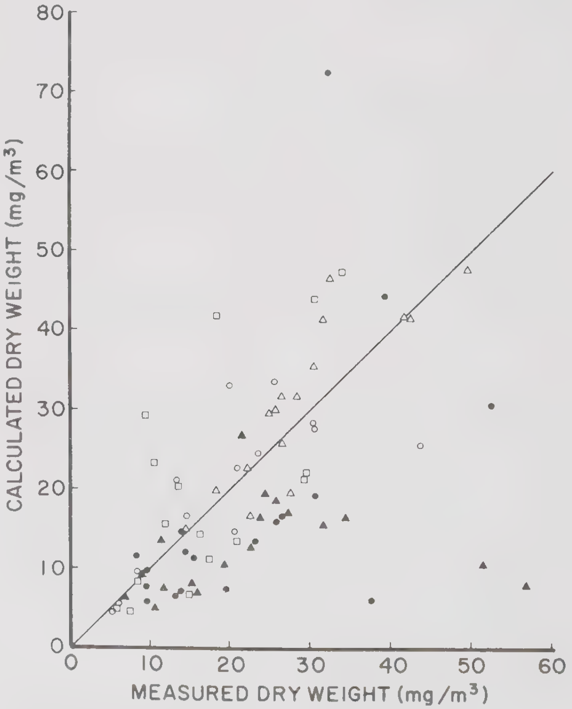

FIGURE 8.—The relation of calculated to measured dry weight concentration for all sampling blocks. Calculated dry weights were derived from species group density estimates and dry weight factors (Table 6). The line indicates equality of the two scales □ Cruise 1; ○ Cruise 2; △ Cruise 3; ▲ Cruise 4; ● Cruise 5.

cruise sets has slopes similar to the line. Variation is wide, but there are only four serious discrepancies. Whatever the reasons for these discrepancies, the four blocks were excluded from calculation of the relative contributions of species groups to dry weight concentrations for day and night cruise periods.

Table 9 shows the averages of dry weights calculated for each species group for each cruise period, and for all cruise periods pooled by day and night. "Calculated" sample concentrations, obtained by summing the values for the four species groups, are compared with the average measured concentrations for the cruise periods in the last two columns. Though the calculated concentrations are lower than the measured concentrations for all day periods, and higher than the measured concentrations for three of the night periods, the two sets show reasonably good agreement, as do the day and night averages for all cruises together.

The measured sample concentrations for all cruises pooled suggest that, on the average, dry weight was 31% higher at night than during the day. The calculated concentrations suggest that it was 48% higher. Calculated values for the species groups show that the dry weight increase at night is largely attributable to increases in the euphausiid group, with lesser increases in the large copepods and also the small copepods. Euphausiids were responsible for more than one-third of dry weight concentration at night, on the average, and small copepods for less than half of it. During the day, on the other hand, small copepods accounted for about three-fourths of dry weight concentration, with most of the remainder divided between large copepods and chaetognaths.

VARIATION WITH TEMPERATURE AND DISTANCE FROM LAND

The data for each of the four species groups, and for dry weight, were examined for possible relationships with the independent variables, temperature, miles from nearest land (including islands), and miles from nearest point on the mainland. Regressions were in the form $\log Y = a + bX$, where $X =$ the independent variable and $Y =$ the dependent variable. Small copepods, large copepods, and dry weight showed significant trends with temperature, and chaetognaths showed significant trends with distance from land (Table 10). For euphausiids, night values alone, as well as day and night values together, were tested but neither demonstrated significant trends.

The two copepod groups and dry weight all show an inverse relation with temperature, but in all cases the trends are largely attributable to changes occurring in 1961, as a comparison of nighttime cruise medians with average cruise temperature shows (Table 11). The decline in

TABLE 9.—Calculated average dry weight fractions (mg/m³) and percentages for species groups by cruise and day (D) or night (N) period.

	Small copepods		Large copepods		Euphausiids		Chaetognaths		Average sample dry weight	
	mg/m³	%	mg/m³	%	mg/m³	%	mg/m³	%	Calculated mg/m³	Measured mg/m³
1D	6.46	*70.9*	0.26	*2.9*	0.26	*2.9*	2.13	*23.4*	9.11	13.04
1N	7.70	*26.1*	3.49	*11.8*	14.88	*50.5*	3.41	*11.6*	29.48	20.87
2D	8.54	*61.4*	2.18	*15.7*	0.36	*2.6*	2.84	*20.4*	13.92	18.02
2N	9.29	*35.7*	4.08	*15.7*	11.83	*45.5*	0.79	*3.0*	25.99	22.24
3D	20.07	*88.3*	0.73	*3.2*	0.63	*2.8*	1.29	*5.7*	22.72	22.94
3N	25.74	*68.7*	3.70	*9.9*	6.99	*18.7*	1.03	*2.7*	37.46	34.01
4D	6.05	*62.6*	0.97	*10.0*	0.35	*3.6*	2.30	*23.8*	9.67	15.66
4N	8.88	*51.0*	1.50	*8.6*	4.95	*28.4*	2.07	*11.9*	17.40	24.51
5D	7.56	*66.4*	2.93	*25.7*	0.28	*2.5*	0.61	*5.4*	11.38	16.72
5N	8.52	*47.7*	2.09	*11.7*	6.86	*38.4*	0.41	*2.3*	17.88	24.09
Average D	9.74	*72.9*	1.41	*10.6*	0.38	*2.8*	1.83	*13.7*	13.36	17.28
Average N	12.03	*46.9*	2.97	*11.6*	9.10	*35.5*	1.54	*6.0*	25.64	25.14

TABLE 10.—Regressions of median block densities and dry weight concentrations on temperature and distance from land.[1]

Regression	N	a	b	s	r
Small copepods on temperature	83	5.38	—.105*	.23	.54**
Large copepods on temperature	78	3.23	—.101*	.52	.26*
Dry weight on temperature	78	2.46	—.067**	.22	.40**
Chaetognaths on distance to mainland	85	1.99	—.013**	.53	.31**
Chaetognaths on distance to nearest land	85	2.02	—.020*	.54	.22*

[1] N = number of sampling blocks; a = intercept; b = slope; s = standard deviation about the line; r = correlation coefficient.
* $p = 0.05$.
** $p = 0.01$.

TABLE 11.—Average temperatures, median copepod densities, and median dry weight concentrations for the night periods of each cruise.

Cruise date	Temperature	Small copepods	Large copepods	Dry weight
	° C	no./m³	no./m³	mg/m³
9/27/61	18.9	2,542	42	18
10/10/61	18.2	3,325	101	21
11/17/61	15.9	10,281	77	32
10/ 2/62	18.6	3,504	21	25
11/20/62	16.1	3,750	30	23

water temperature was approximately the same in both years. The copepod values and dry weight consequently show a strong inverse relation with temperature and date for 1961 but not for 1962.

The chaetognaths show inverse trends with distance from the mainland and from nearest land, but the former is the more significant of the two. The relationship with distance to nearest land includes many of the distance measurements to the mainland, of course, and it is possible that these are largely responsible for the significant relationship with distance to nearest land. The geographical distribution of all chaetognath block medians (Figure 9) shows that distance from the mainland is the more pertinent independent variable. Low densities occurred at all distances beyond 7 miles, whereas the highest densities did not occur farther offshore than 14 miles, with a single exception. It can be seen that density was far more variable near the mainland than offshore.

DISCUSSION

The food potential of plankton for pelagic fishes depends on the relation between the average density of some or all species groups over an area and the rate at which the fishes can feed on these species groups. Since median density of the more common species groups varies widely within the space of a few months for the area surveyed in this study, it is probable that food potential of near-surface plankton off southern California fluctuates appreciably within short time intervals. However, there were marked small-scale variations in the distributions of densities associated with the general area levels, and the general level would not be an appropriate index of food potential if fishes tend to orient to small-scale features of distribution.

Although the association of range with median for sampling blocks of 51.8 km^2 demonstrates that densities vary, sometimes widely, within the blocks, the medians of blocks of this or some similar size probably constitute a scale of sufficient resolution for assessing the food potential of plankton over a large area. Maximum values within the blocks are not likely to be impressively greater than the median. If the median of large copepods is 175/m^3, the block can be expected to have, on the average, a maximum density of 245/m^3 representing an area of 2.6 km^2 (1 square mile) within the block. If the median of euphausiids is 90/m^3, the block can be expected to have a maximum density of 130/m^3 for 2.6 km^2. Blocks with such medians are usually rare, and the medians, as well as the maximum values, are likely to be considerably higher than the densities in most blocks in the area. The medians would slightly underestimate the food potential of such blocks only if plankton feeding fishes tend to orient to the highest densities within the space of 20 square miles.

The distributions of sampling block medians, which were skewed unless general area level was very high, suggest that even under the poorest general conditions relatively high densities of organisms are likely to exist in some small portion of the survey area. Small copepods, for example, showed a few occurrences of blocks with medians above 6000/m^3, and one

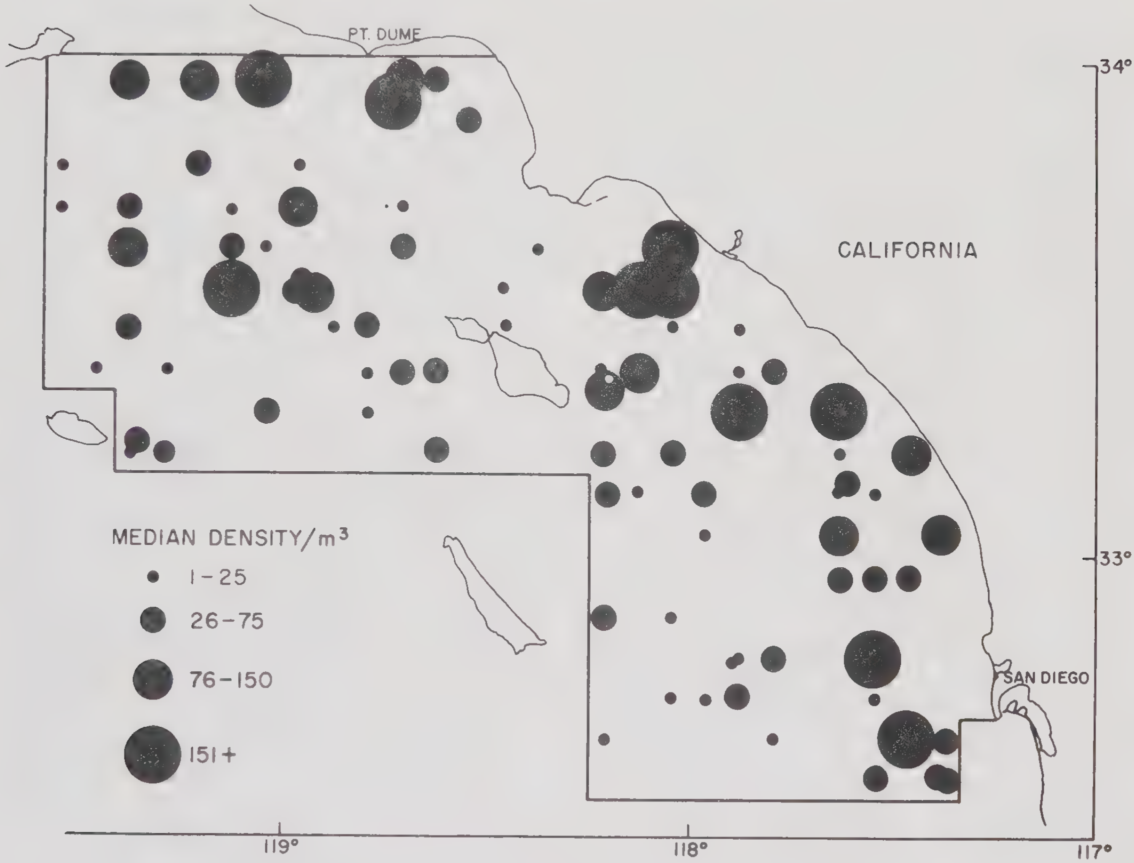

FIGURE 9.—Geographical distribution of chaetognath medians for all blocks on all cruises.

with a median above 9000/m³, when the general area median was about 3000/m³. Large copepods showed a few occurrences of blocks with medians well above 200 when the general area median was 50/m³ or less. Euphausiids showed occurrences of blocks with medians above 75/m³ when the general area median was between 25 and 40/m³. It seems probable, in other words, that high crustacean densities are always present somewhere in the area. At the lower general levels they would be scarce but perhaps as much as three times higher than densities over most of the area.

The data indicate that higher densities of chaetognaths are most likely to occur near the mainland, but they failed to demonstrate such trends for the three crustacean groups. They indicate only that the crustaceans, and dry weight, may sometimes be at higher levels where and when temperatures are relatively low. Regressions with temperature show, for example, that the density of small copepods was 6400/m³ in 15° C water, on the average, as compared with 2400/m³ in 19° C water, and that dry weight concentration was 29 mg/m³ in 15° C water, but only 15 mg/m³ in 19° C water. Since variation associated with these trends is wide, it can only be concluded that water of low temperature may sometimes, though not always, contain much higher standing crops of zooplankton than are likely to be found in warmer water in the survey area.

Dry weight factors were determined for the different species groups because it is impossible to estimate the relative nutritional value of such groups in the plankton on the basis of organism counts alone. In general, the near-surface zooplankton had a dry weight equivalent of about 25 mg/m^3 at night, which was approximately 30% greater than the average daytime level. Small copepods were the dominant fraction during the day and increased only slightly at night. Most of the nighttime increase in dry weight is attributable to the appearance of euphausiids, which were estimated to have a dry weight equivalent of 9 mg/m^3, on the average, as compared with less than 1 mg/m^3 during the day. There was some deviation from this general pattern among the five cruises. Differences between and within sampling blocks were not described in terms of dry weight. The general differences are enough to show that the nutritional potential of the plankton, in terms of dry weight for any set of samples, would depend on the extent to which fishes do or do not feed selectively.

However they are interpreted, it must be noted that the dry weight equivalents of the samples taken in this survey, aside from the possible loss of weight in Formalin preservation, may not represent the whole of the biomass utilized by some plankton feeding fishes near the surface. They contained almost no zooplankters smaller than 0.2 mm in length and relatively little phytoplankton. The comparison in Table 12 indicates that such smaller organisms may constitute a considerable fraction of the biomass.

Beers and Stewart (1967) sampled the euphotic zone with a towed pump on a line of stations off San Diego. Water was strained successively through 202-, 103-, and 35-μ cloths to estimate quantities below each cloth. Leong and O'Connell (1969) estimated from the resulting data that phytoplankton and zooplankton passing through the 103-μ cloth represented average dry weight concentrations of 25 and 3 mg/m^3. The 103-μ cloth was approximately the same mesh size as the filtering screens used in the present survey. The material retained between the 103- and 202-μ cloths of Beers and Stewart is here judged to approximate the size range, 0.2 to 1.0 mm, and the numerical estimate for their innermost station, when converted to dry weight by the constant, 2.5 mg/1000 organisms, yields a concentration similar to the daytime average for crustaceans in this size range in the present surveys.

TABLE 12.—Comparison of dry weight values (mg/m^3) for different length ranges of planktonic organisms in two towed pump studies.

	Period	Group	Length range (mm)		
			<0.2	0.2-1.0	>1.0
Beers and Stewart (1967)	Day only	Phytoplankton	25.1	0	0
		Zooplankton	2.9	8.9	0
Present survey	Day	Crustacean	0	9.7	1.8
	Night	Crustacean	0	12.0	12.1

It appears that material smaller than that collected in the present survey might represent a dry weight approximately two to three times as great as that that was collected. Adjustment for the smaller organisms in questions of nutritional potential would depend on selectivity in the feeding of various fishes.

It is difficult to judge whether the dry weight values attributed to organisms larger than 1 mm in the above comparison fully represent the biomass of larger plankton organisms near the surface that can be utilized by plankton feeding fishes. Such fishes probably take crustaceans larger than collected by the pump when opportunity arises. It can only be restated that euphausiids larger than those sampled are relatively rare close to the surface. Five of the 1-m-mouth-opening-net tows taken by Ahlstrom and Thrailkill (1963) through the upper 100 m or so were composed largely of crustacean material. From the data given they were estimated to represent dry weight concentrations averaging 3.5 mg/m^3. The figure is in the range of day and night concentrations for the pump samples, but the comparison is uncertain because of differences in the location as well as the depth of sampling.

The above discussion implies that estimating the food potential of plankton for fishes must depend as much on information concerning the feeding behavior of the fishes as on information concerning the abundance and variability of the plankton. The data given here on plankton variability are intended as a basis for interpreting hypotheses that may arise from laboratory or field studies of feeding behavior.

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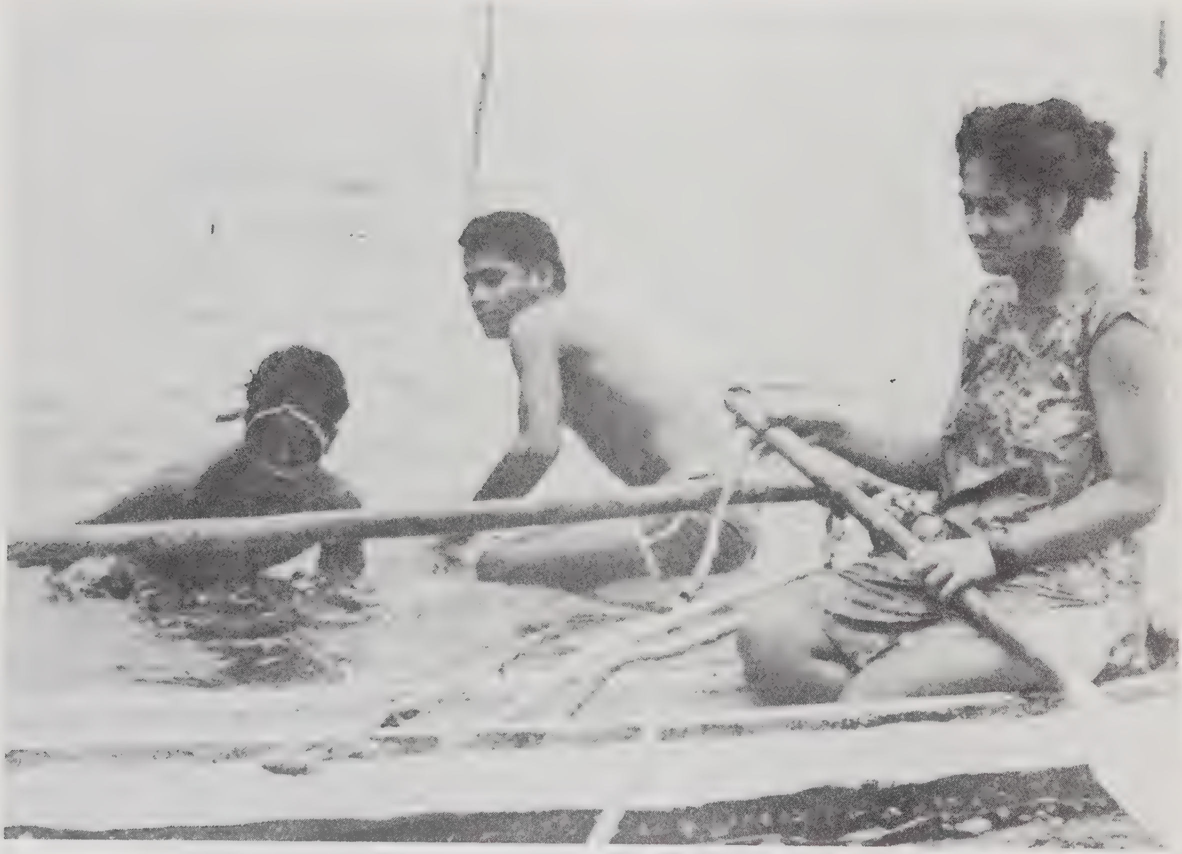


A Samoan woman paddles the canoe (paopao) as two companions tend a fish trap constructed of wire netting on the reefs near Pago Pago, American Samoa.

American Samoa Fisheries

SAMOA AND PAGO PAGO (pronounced Pango Pango) are perhaps best known from the short story by W. Somerset Maugham as the place where the notorious Sadie Thompson once plied her trade. Indeed, one may wonder why we have a chapter on the fisheries of American Samoa. Many Americans are probably not aware that important fisheries are conducted from these romantic South Pacific islands.

The Samoa Islands are ethnically and culturally allied but politically divided. The seven islands known as American Samoa became a territory of the United States in 1900 when leading Samoan chiefs negotiated a deed of cession. Other islands in the Samoan group—located about 80 miles to the west—comprise Western Samoa, which is now an independent nation.

American Samoa, with a population of 27,000, includes Tutuila, where Pago Pago is located; Aunu'u; the Manua group, which includes Ta'u, Olosega, and Ofu; and Swains and Rose, both of which are tiny coral atolls. The combined land area of these islands is only 76.2 square miles, or about one-sixteenth the land area of our smallest state, Rhode Island.

The main islands, which are of volcanic origin, rise abruptly from the sea in a series of ridges. Tutuila, the largest, is a nondescript, irregularly shaped piece of land about 18 miles long and 6 miles across at its widest point, located near latitude 14° S. and longitude 170° W. It is many hundreds of miles away from any familiar points of reference, being about 2,300 miles southwest of Hawaii and 1,600 miles northeast of New Zealand.

The one exciting feature of Tutuila is a drowned valley on the southern side—Pago Pago Bay, which nearly bisects the island. The bay is without doubt the finest and most beautiful harbor in the South Pacific. It is large and deep enough to accommodate vessels of any size, and is now the home base for a fleet of commercial longline fishing boats.

Though the ages of the Samoa Islands are not known, geologically the most recent is believed to be the westernmost, Savaii, in the Western Samoa group. The oldest islands are the easternmost Manua group of American Samoa. The submarine features of the Samoa Islands are like that of many other volcanic islands. Hardly any Continental Shelf exists around the islands and water depth plunges fairly rapidly away from shore. Narrow coral reefs, irregularly interrupted in places, encircle the high islands. The islands are bathed by the waters of the warm, sluggish South Equatorial Current system. The temperature at the sea surface around the islands changes with seasons from about 75° F. to 86° F.

THE COASTAL REEF-FISH FAUNA of the Samoa Islands is part of the vast marine zoogeographic fauna centered around the East Indies. The shallow coastal waters in and around the coral reefs of Samoa abound with many colorful fishes. More than 600 species of fish are known to inhabit these waters. Although the species are numerous, only a few are of economic importance.

Unlike temperate regions—where relatively few species are the basis of large fisheries—in tropical Samoan waters the myriad of fish species support almost no local or indigenous commercial fisheries. The customs, mores, and traditions of the Samoan people probably precluded the need for commercial fishermen. The extent to which the ancient traditions have been diluted is unknown but in Samoa a custom exists where many material goods—including necessities for subsistence, like farm produce and fish—are shared by the families in villages.

The tradition of sharing is part of what is known as the chief (matai) and family (aiga) system. Aiga (pronounced ainga) has a broad definition and includes not only the immediate family group of father, mother, and children, but all distant relatives. The aigas can assume huge proportions, for a typical Samoan family is

large even without including all relatives.

Apparently, at least at one time, certain kinds of work including house building and fishing were traditionally done by members of guilds. Some of the fishing guilds were composed of members of royal lineage. There were also village fishing guilds. The rights of membership in the royal guilds were handed down from generation to generation. The Samoans are able to trace the origin of the guilds to the original senior fishermen, partly historical and partly legendary.

The catches made by fishing guilds were shared by the aigas in the villages. It is uncertain whether members of the fishing guilds received any monetary payment for their services, but it appears that members of builder guilds did receive food and monetary gratuities. It is certain that many customs and traditions are being altered or lost, especially in the more urbanized sections of American Samoa. One authority on Samoa, however, noted in his book published in 1962 that a number of fishing guilds still existed. It is probably true that some form of organized fishing is still practiced in outlying villages.

METHODS EMPLOYED BY AMERICAN SAMOANS TO CAPTURE FISH AND SHELLFISH from coastal areas surrounding the islands have changed little over the years. Te Rangi Hiroa (Peter H. Buck), who visited American Samoa in 1927 on a Bernice P. Bishop Museum (Honolulu, Hawaii) expedition, described Samoan fishing methods and implements in great detail.

Of interest is Buck's account of Samoa's only "high-seas fishing" endeavor, "bonito" fishing as practiced in those days. Bonito (atu), as skipjack tuna is known locally, was fished from a bonito canoe (paopao). During the season, a fleet of several canoes went out during the hours of darkness in order to be on the fishing grounds just beyond the reefs by daybreak. Each canoe, with up to three men, had a pole with a barbless hook—fashioned from pearl shell—trailing in the water.

After locating a school of skipjack, by first sighting a bird flock or by noticing ripples on the water surface, the steersman headed the canoe into the midst of the school. When a skipjack was hooked, the rod was lifted by the steersman, who swung the fish into the canoe. "Atu-e" ("a skipjack") was the cry that then rang out through the fleet. The fishermen continued furious paddling in order to keep pace with the rapidly moving schools. There were times when the canoes worked all day without any luck. On occasions the canoe came home so loaded that the fishermen had to guide their craft in through the reef by swimming alongside. This primitive type of skipjack fishing is still practiced by the Samoans, particularly those on Manua. The canoes, however, leave the confines of sheltered waters only during the calmest weather.

As in other parts of Oceania, Samoans comb the reefs for fish and shellfish in various ways. They may simply grope between the rocks and coral with bare hands or use devices like spears, traps, nets, and hooks. Bamboo pole fishing is a popular method of catching reef and inshore fishes. It is a common sight to see

A Samoan woman cracks a piece of coral to extract a hidden sea urchin. Women and youngsters comb the reefs around American Samoa for many kinds of shellfish for use as food and to make shell leis and trinkets that will be sold to tourists. Few Samoans have commercial fishing enterprises.

Samoans fishing off the piers surrounding Pago Pago Bay at night, using the light of a gas lantern to attract the bigeye scad, a favorite food fish. During the night Samoans may handline from canoes for bigeye scad and during the day for other species like the barracuda and dogtooth tuna.

Traps made of wire netting are constructed along the reefs, usually in or near a small channel. Long sections of wire netting are strung out in a V-shaped pattern, with a circular or rectangular enclosure about 5 to 10 feet in diameter at the apex. The traps are used principally to capture such fish as mullet and jacks. Set nets and throw nets are used over the reefs and sand flats for mullet and other estuarine species. Spears are used to capture fish and octopus.

Shellfish are collected both day and night along the edges of the reef for food and for making shell leis and trinkets, which are sold to tourists.

Nearly all fish and shellfish taken are for personal consumption. On occasion, when the catch is larger than the amount needed, the Samoans may place some on sale along the roadside.

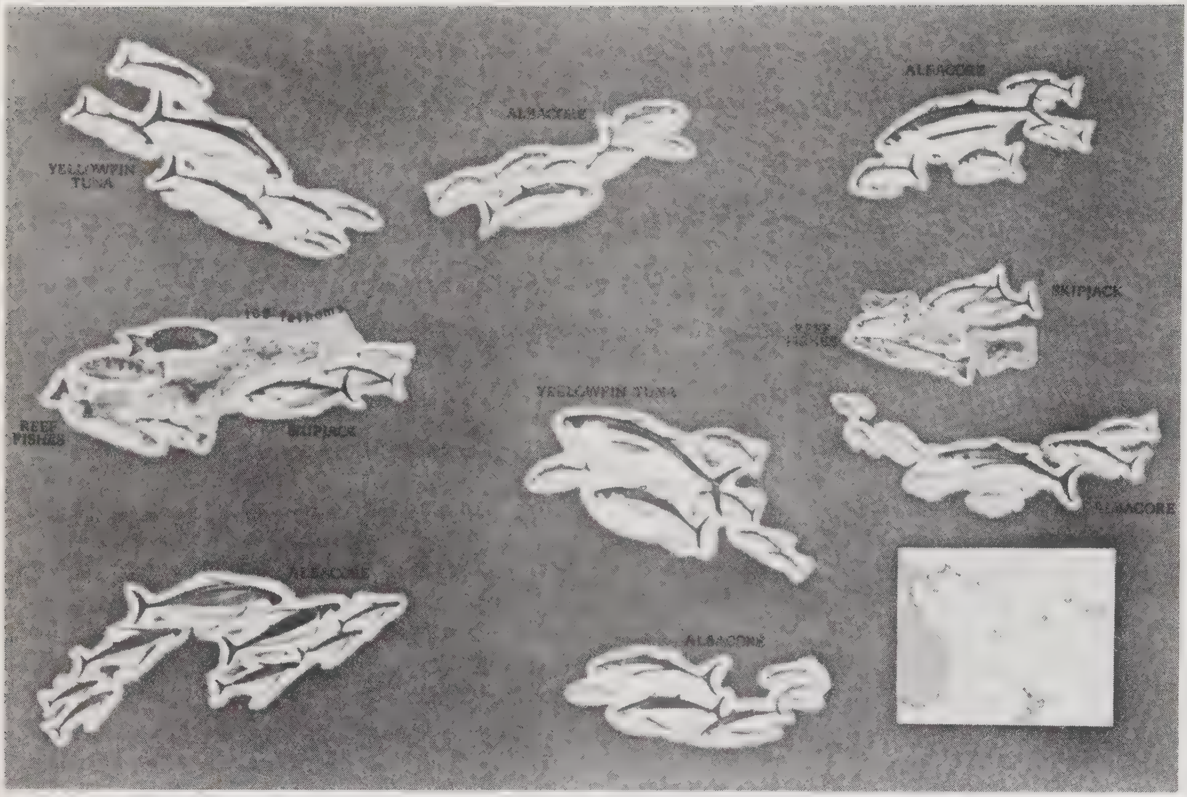
In 1966 a fish market was built at the public marketplace in Pago Pago by a group of Samoans. The market is equipped with a walk-in freezer and two chest freezers. Since local commercial fisheries do not exist, frozen fish obtained from the tuna canneries is being placed on sale. Fish taken trolling by two charter boats of the corporation, which owns the fish market, are also placed on sale, though this is not a regular source of supply. The corporation hopes that the Samoans will be encouraged to sell reef fishes, lobsters, other shellfish, and other fishery products there. This development may encourage the Samoans to develop their own commercial fishing enterprises.

A description of the fisheries of American Samoa would not be complete without mentioning palolo, although it is not even of potential commercial importance. Palolo are wormlike sacs of eggs and sperm of a sea annelid. The sacs are freed by adults at predictable times either in October or November. Freed sacs swarm to the surface in wriggling masses. The sacs are about a sixteenth of an inch in diameter and may be a foot or more in length. Female palolo are filled with eggs which are green; male sacs are filled with reddish-brown sperm.

Palolo are greatly esteemed by Samoans, who look forward to the annual surface swarming with great anticipation. The appearance at the surface—usually once a year and then only for a few hours in the middle of the night—creates great excitement as young and old alike, armed with scoop nets, pails, and other simple implements, go out on the reefs to collect their share of the delicacy.

Large quantities of palolo are eaten raw by the natives. Palolo—characteristically salty—can be cooked with chopped onions or scrambled with eggs.

THE COMMERCIAL FISHERIES OF AMERICAN SAMOA are conducted by outsiders. In 1949, even before it was known that a sizable tuna resource existed in the South Pacific Ocean, or before there was any significant exploitation of this resource, the potentials were recognized by a company known as Island Packers. It leased land and buildings from the Government of American Samoa to install a small cannery along the north shore of Pago Pago Bay. An attempt was made to catch tunas in waters near Samoa by conventional American fishing methods—live-bait fishing and purse seining. These methods



American Samoa fisheries are of two types: Subsistence fishing is conducted by natives in coastal water for reef fishes and sometimes skipjack tuna. Commercial fishing on the high seas to supply raw materials—principally albacore and yellowfin tuna—to modern canneries is conducted under contract by Japanese, South Korean, and Taiwanese longline vessels.

failed and the cannery never began operation.

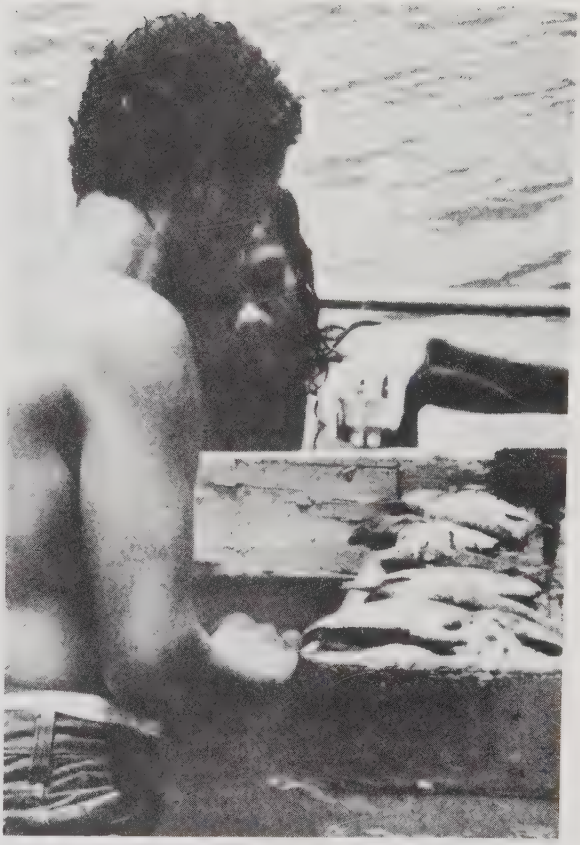
Rather than have the cannery equipment dismantled and sold abroad, the Government purchased it and offered it for lease in the hope that its operations would some day contribute to the economy of the Islands. In 1953, the Van Camp Sea Food Co. of Terminal Island, Calif., obtained the lease with a renewal option. In the following year, operations began with fish delivered under contract by a small fleet of Japanese longline vessels. In 1963, a second tuna packing firm, Star-Kist Samoa, a subsidiary of Star-Kist Foods of Terminal Island, began operations with a cannery adjacent to the Van Camp plant.

Though surface fishing methods failed to catch tunas, the Japanese longline method of fishing for deep-swimming tunas has been effective in harvesting the tuna resources that abound in the vast extent of the South Pacific. In longlining a long series of baited hooks is lowered to depths of as much as 100 fathoms or more. This method of fishing for the canneries is being used today by fleets of vessels from Japan, the Republic of Korea (South Korea), and the Republic of China (Taiwan).

According to the 1967 Annual Report of the Governor of American Samoa, about 2.4 million cases of tuna, 324,000 cases of pet food, 2.4 million pounds of frozen fish, 3.9 million pounds of fishmeal, and 890 cases of canned wahoo were produced in American Samoa in that fiscal year. These products were valued at $27.2 million, of which canned tuna was $25.6 million. Fishery products accounted for over 90 percent of the total value of products shipped from American Samoa to the United States that year. The tuna canneries provide jobs for approximately 950 Samoan men and women, thus giving the economy of American Samoa a major boost.

The American Samoa facility was probably one of the earliest "overseas" American tuna canning or freezing installations to be established. Besides having this distinction, the Samoa-based fishery has a unique atmosphere. Envision if you will bustling unloading activities at the docks of the tuna canneries in picturesque Pago Pago Harbor. Tuna canneries there are as modern and clean as any cannery anywhere in the world. Inside, in the butchering rooms brawny lava-lava clad youths adroitly handle huge tunas. Neatly dressed Samoan women trim and pack tuna at rows and rows of packing lines. All this is set in an idyllic and otherwise slow-paced Polynesian island.

The foreign fishing vessels, either individually or through fishing companies, enter into contracts with the American tuna processors for periods up to 2 years. Foreign fishermen add much color to the local scene. On the day of departure at the end of a contracted period of fishing, Japanese fishermen swathe their vessel with colorful banners. Before leaving, the vessel makes several swings around Pago Pago Harbor—ship's horn blaring and loudspeakers echoing strains of Auld Lang Syne (Hotaru No Hikari). While working at dockside, foreign fishermen wear clothing that is traditionally worn in their home countries. The Taiwanese fisherman may wear a coolie hat and the Japanese fisherman may have a towel (hachimaki) wound around his head.



Young Samoans sort a catch of reef fishes taken with handline from a canoe. This simple fishing method is typical of the subsistence fisheries in Samoa today.

Japanese longliners landing at American Samoa are of the same type as those that ply the world's seas fishing subsurface waters for tunas and for marlins and other billfishes. The design of a Japanese longliner provides a large space forward that is free of excess deck structures. Here in this large deck space is where the longline gear is hauled in and the fish landed, sorted, and butchered, if necessary, for storage in the holds below. Japanese longliners fishing out of Samoa range from about 70 to 355 gross tons, and may be constructed of steel or wood.

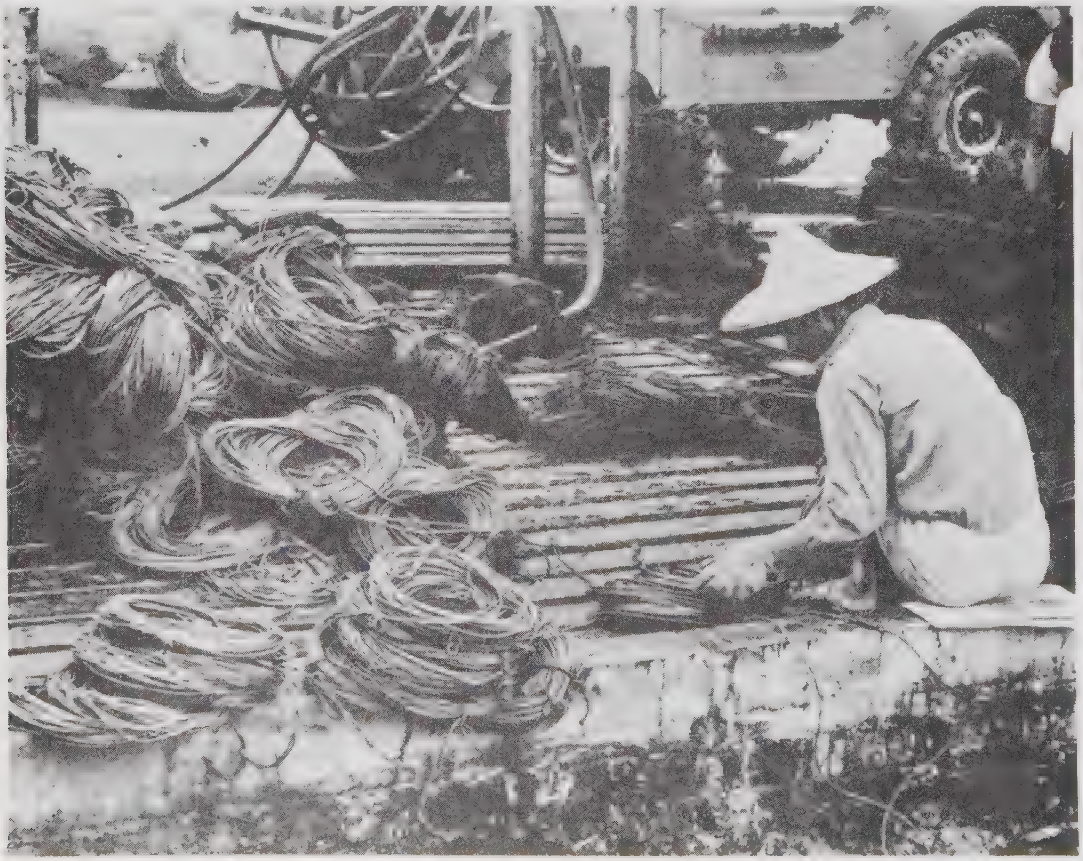
The Korean longliners are of relatively recent construction and are all built of steel along the same lines as the Japanese vessels. They are 97 to 263 gross tons.

The Taiwanese vessels are constructed of wood or steel. The wooden vessels are generally small (between 20 to 40 gross tons) and are of a different design than that of the steel vessels. The steel vessels range up to 320 gross tons and are similar in construction to the Japanese and Korean longliners.

The number of vessels and the composition of the fleet have varied over the years. Originally the fleet was composed entirely of Japanese vessels—seven in 1954. Vessels from South Korea joined the fleet in 1958 and Taiwanese vessels in 1964. In 1967, 257 vessels fished from American Samoa for varying lengths of time. In the last quarter of 1967, the 175 longliners then in operation were composed of 42 Japanese, 52 Korean, and 81 Taiwanese vessels.

On the longliners based at American Samoa, crews range from 12 men on small Taiwanese vessels to over 30 men on the larger vessels. This may appear like overly large crews. So many are needed, however, because of the long hours required to fish the longline gear; the crews work in shifts.

Outsiders operate the large-scale modern commercial fisheries of American Samoa. Here, a Taiwanese fisherman prepares tuna longline gear for a voyage out of Pago Pago. Fishing trips may last up to 30 days and range up to 2,000 miles from port.



Taiwanese fishermen unload albacore from a tuna longliner at an American cannery in Pago Pago. Fishery products, mainly canned tuna to be shipped to the United States, were valued at over $27 millon in fiscal year 1967.

On a typical fishing day the lines are set at dawn, and this takes about 1 to 2 hours. Up to 400 or more baskets are set each day. The longline, which is put out in a straight course and may stretch over 50 miles, is allowed to drift free with the current. The line is retrieved starting at about noon and this operation may take over 12 hours on a day when the catch is good. It is not unusual for a hauling operation to end at 2 a.m. the next morning. While the fish are being hauled aboard, other crewmen begin processing the catch for storage in refrigerated holds. Albacore are stored in the round, but the larger fish—yellowfin and bigeye tunas and all the billfishes—are gutted. The entire routine of setting, retrieving, and storing is repeated again only about 2 hours after the catch of the previous day is put away. The longliners may observe this routine for 30 consecutive days on a fishing voyage.

ALBACORE COMMANDS THE HIGHEST PRICES AT THE CANNERIES and is therefore the principal target of the tuna fleets. Fishing grounds are generally chosen where albacore are most abundant rather than where the largest catch of all tuna species can be made. On occasion, even less-choice fish that are caught will be discarded to make storage room for the premium albacore.

Yellowfin tuna is the second most important species delivered to the canneries. Other species taken by the fishery include bigeye tuna, southern bluefin tuna, skipjack tuna, wahoo, billfishes, sharks, and other miscellaneous pelagic species.

Of the tunas taken on longline, only albacore and skipjack tuna are wholly acceptable for canning. Some of the larger yellowfin, bigeye, and southern bluefin tunas (those over 100 pounds) have a distinct tendency to result in packs which are too dark to meet the high standards set for canned tuna. The wahoo is canned specially for the local American Samoans and this novel product has found ready acceptance. A small quantity (perhaps under 200 tons) of the larger tunas, billfishes, and other species is sold to the Samoans by the cannery operators. About another 1,000 tons of these fish are purchased by Japanese firms and transshipped to Japan for processing into fish hams and sausages.

Albacore landings by the Samoa-based fleets have gradually increased from an estimated 745,000 pounds in 1954 to over 62 million pounds in 1967. In 1968, landings declined to 39 million pounds.

Albacore are caught throughout the year, although in some years slightly better landings are made during the latter half of the year. This albacore fishery, therefore, may truly be classed as a year-round fishery in contrast to the highly seasonal North Pacific albacore fisheries off the coasts of the United States and Japan.

Albacore are streamlined, fast-swimming pelagic fishes that are distributed over a large area. At first the longliners fished relatively close to the Samoa Islands. As the number of vessels increased, the fishing grounds expanded and, by 1956, the vessels were venturing far afield to waters southeast of the Tonga Islands, some 700 miles away. The longliners extended their fishing grounds eastward about 2,000 miles to the Marquesas Islands in 1958, which was the year of greatest geographical expansion. At the end of 1966 the fishing grounds covered an area in excess of 7.5 million square nautical miles between the Equator and latitude 30° S. and from longitude 175° E. to longitude 120° W.

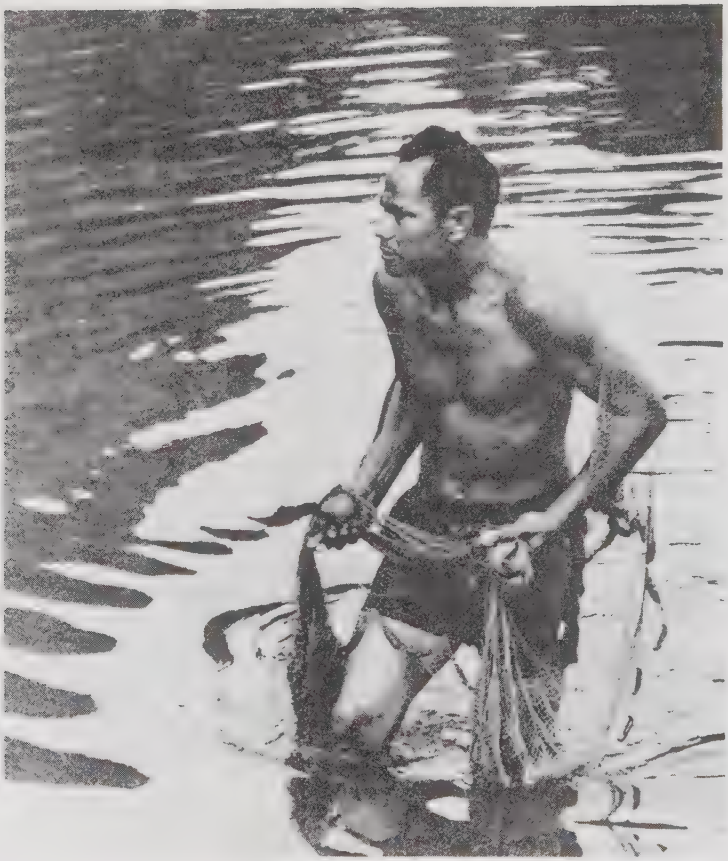
The fishermen have learned many things about albacore through their own experiences and the collective experiences of other fishermen. Keen observations have been made on the movements, the geographical size distribution, and the abundance of albacore. Most of the fishing masters make use of these observations to select fishing grounds. Smaller vessels restrict their fishing close to home base, because they are faced with weather conditions and problems of supply.

Albacore landed in Samoa weigh about 20 to 75 pounds, and average around 40 pounds. Sexual maturity is attained between the ages of 5 and 6, or when the fish are about 30 pounds. Most of the albacore taken by the Samoa-based fishery are therefore mature fish. Studies of their reproductive habits have shown that they spawn over an extensive area in the central South Pacific, generally between latitudes 10° S. and 20° S., and that the spawning season occurs during the south-

Samoans are employed by two American tuna processing companies based in the Territory. A Samoan dressed in the age-old lava lava swings a 40-pound albacore into a cannery cart.

ern summer months between November and March.

The catch rates of albacore have shown some decline during the last decade. Initially, this decline was due to a decrease in numbers of older, larger fish in the population—which is to be expected when a previously unexploited or lightly exploited population is subjected to heavy fishing pressure. A decrease in albacore landings since 1968 is partly the result of a shift in emphasis toward yellowfin tuna during certain months when fishermen prefer to fish calmer "yellowfin waters" closer to American Samoa rather than the more distant waters for albacore. To mon-



The cast net is a common gear used by Samoans to catch fish for the dinner table.

itor the effects of the longline fishery on the resource, the staff of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, is regularly collecting data on catch, fishing effort, and biology.

Our present state of knowledge indicates that at least two separate populations of albacore exist in the Pacific Ocean, one in the North Pacific and the other in the South Pacific, with little, if any, intermingling across equatorial waters. The Samoa-based fishery is of course exploiting the South Pacific population, a population separate from the one being fished by U.S. fishermen in the eastern North Pacific off California, Oregon, and Washington.

Let us consider some of the differences between the Samoa-based fishery in the South Pacific and the American fishery in the northeastern Pacific. Foremost, albacore landed in Samoa are large, mostly mature fish. These large fish are found at great depths in tropical and subtropical waters, and thus can be captured only by the specialized longline gear. In contrast, most of the albacore landed by U.S. fishermen off our Pacific coast are smaller (under 20 pounds), immature fish from the North Pacific population. Smaller fish are generally found at the surface in temperate waters where they are taken by surface trolling, live-bait fishing, or purse seining.

FROM THE STANDPOINT OF SAMOA'S ECONOMY it would be highly desirable for Samoans to gradually replace foreign fishermen in the tuna fishery. Samoan men are big, husky, and agile. They have an inherent love for the sea. Like other Polynesians, they too have a history of being seafarers. It would seem that American Samoans possess all the necessary ingredients to become expert longline fishermen.

The Samoans are capable plant-workers, having adapted rapidly to modern industrial requirements, but they have shown no great inclination to become high-seas tuna fishermen. Perhaps because of the nature of the fishery—which necessitates long absences from home of 30 to 40 days on a single trip and the extremely difficult working conditions—Samoans are reluctant to become longline fishermen.

The lease agreement between the tuna cannery and the Government of American Samoa in 1953 included a provision to train Samoans in tuna fishing with a view to eventually using local people to catch the fish, as well as to process them. In 1961, the Van Camp Sea Food Co.–Samoa, obtained a longline vessel from Japan and operated it with a crew of eight Japanese and 15 to 18 Samoan trainee-fishermen. In 2 years the vessel made 10 fishing trips, and 106 Samoans tried their hand at becoming tuna fishermen. Only one Samoan remained with the ship long enough to become a good fisherman.

Other types of fishing, say for skipjack tuna in coastal and nearby offshore waters, may be more suitable for the Samoans. At present, local fishing is on such a small scale that it does not begin to meet the demand of the local population for fresh fish. Although the sea around them abounds with fish, Samoans depend more on canned corned beef than fish for their protein needs. It is clearly of economic advantage to the Samoans to develop commercial fisheries of their own. A thorough and systematic investigation of the aquatic resources may lead to the development of a skipjack fishery similar to the one that now exists in the Hawaiian Islands. Catches of skipjack and possibly other species in excess of local needs might be sold to the canneries for processing or may possibly be exported.

STEPS TO EXPAND LOCAL FISHERIES are now being taken by the Government of American Samoa under the provisions of the Commercial Fisheries Research and Development Act of 1964, which provides Federal funds to supplement State funds for fishery development. American Samoa is included under the provisions of this act. During the fiscal year ending June 30, 1969, Federal funds of $77,100 were allocated to American Samoa. Since the program was started, the cumulative total has been $241,000.

The Government of American Samoa in 1966 created a position for a Fishery Development Officer to supervise the program. A small fishing vessel was purchased in 1967 for exploratory work under the command of a fisherman-captain experienced in various fishing techniques that may be suitable for Samoan waters. The success of this program should go a long way in stimulating the economy of American Samoa by creating more job opportunities both for fishermen and cannery workers.

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7139

THE ECONOMICS OF OPERATING A WETFISH SEINER

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If we are going to harvest the anchovies and mackerel in the California Current region, we will have to do something about the fleet. The fleet is small, and the boats are old. With this in mind, the Operations Research Group at FOC, La Jolla decided about a year and a half ago to look into the economics of operating a wetfish seiner. We collected data on costs and earnings correlated with landings for 22 boats for the period 1963 through March 1968. Altogether I examined about 1,000 monthly settlement sheets, as well as various financial records.

Our study had three objectives: 1) to describe and document the economic condition of the fleet, 2) to construct a costs and earnings model, and 3) using the model, to examine the economic feasibility of expanding the fleet, either through recruitment of surplus vessels from other fisheries, or through new construction.

I presented a summary of the data on the financial condition of the fleet at the MRC meeting in June 1969. Suffice it to say that, as of the first quarter of 1968, the fleet was doing very poorly. Profits were very low on the average, costs were rising, and employment was falling. The data are available in a published paper (Perrin and Noetzel, 1970).

Today I will tell you very briefly about the approach we used in analyzing costs and constructing a predicting model, and I will summarize the conclusions we reached through use of the model about the economic feasibility of fleet expansion and new construction.

We wanted to predict costs, profit, return on investment, and crew earnings for various-sized vessels at various levels of revenue and various catch compositions with respect to species, and we used a straight forward reductionist approach.

We were not able to predict revenue. We could find no relationships in our data between total value of landings and vessel characteristics such as size, fish capacity, or horsepower. We can think of several possible reasons for this. More often than not, the boats are not fully loaded, or even half loaded, when they come in, especially when they are fishing mackerel, bonito, or tuna. This could be expected to reduce the effect of differential size. Most of the fishing is very local, often within 8 or 10 miles or less of port. This would reduce the effect of differential speed. Another possibility is that skill is an over-riding factor. Setting a purse seine requires a great deal of skill, and some captains are certainly better at it than others.

Still another possibility, of course, is that we had insufficient data. We had no effort data correlated with landings. California Fish and Game has now collected such data, and perhaps between-vessel differences correlated with vessel characteristics will become visible after landings have been standardized to effort.

Since we could not predict revenue, we instead predicted costs, profit, etc. at arbitrary levels of revenue over a range including all levels achieved by boats in the fleet in the past and hypothetical higher levels.

In other words, the approach we used was to say, "What would be the costs, profit, return on investment, and crew share for a 150-ton capacity boat landing $100,000 worth of mackerel? What would they be if the landings were half mackerel and half anchovies, or if it were a 100-ton capacity boat, and so on."

Since we are interested in the feasibility of new construction, we asked the questions for hypothetical new vessels, as well as for old vessels of the type now in the fleet.

First, we had to analyze costs. The costs are of two major types; so-called "trip expenses" and "owner costs." Trip expenses are deducted from the gross revenue, and include fuel, oil, salt, ice, airplane spotting, and contributions to the welfare fund, the pension fund, and the patrol agency. Rather than subdividing trip expenses in our analysis, we attempted to relate them *in toto* to amount and species composition of the landings, using the data from the monthly settlement sheets. We did a multiple regression on the data for 1967:

$$Y = 914 + 0.00103X_M + 0.00519X_T + 0.00399X_B + 0.00038X_A$$

where Y = estimated trip expenses for one settlement period, 914 is the Y intercept, X_M = pounds of mackerel, X_T = pounds of tuna, X_B = pounds of bonito, and X_A = pounds of anchovies landed. All the coefficients are significant at P = less than 0.001, and the regression accounts for 75% of the variance. Since we are concerned more with dollars than with pounds, we restated the relation for the annual case as follows:

$$Y = 8{,}052 + 0.0275\ X_M + 0.0419\ X_T + 0.0939\ X_B + 0.0380\ X_A$$

where 8,052 = the intercept for the single settlement case multiplied by 8.81, the average number of settlements per year; X_M = the value of mackerel; X_T = value of tuna; X_B = value of bonito, and X_A = value of anchovies. This says that, per dollar's worth, bonito are the most expensive to catch, tuna and anchovies cost about the same, and mackerel is the least expensive to catch.

$$\text{For anchovies: } \frac{\text{cost}}{\text{value}} = \frac{\$0.00038/\text{lb.}}{\$0.01/\text{lb.}} = \frac{\$0.038}{\$1}$$

So now we can estimate the trip expenses attached to a particular level of revenue and a particular catch composition.

After trip expenses are deducted from the gross revenue in a settlement, the remainder is split between the owner and the crew. In the San Pedro fleet, the owner's share ranges from 36½% to 41½%, depending on the size of the vessel. The owner pays the so-called "owner's costs" out of his share. In our analysis of owner's costs, we used the following categories: parts and repairs, netting and supplies, insurance, payroll taxes, interest, moorage, state and county taxes, depreciation, and a miscellaneous category. For some of these submodels, such as insurance and depreciation, we used deductive methods, for others, such as parts and repairs and netting and supplies, we fell back on empirical equations derived from our data. Most of the estimations are dependent on the characteristics of the vessel and on the level of revenue. Only one, that for netting and supplies, depends on the composition of the catch; it increases by $2 per ton of fish landed, which obviously is quite important when considering anchovy fishing. We had no data for repair costs for new wetfish boats, so we used data for new shrimp boats of comparable size in the Gulf of Mexico.

We then used the cost estimators and predicted profit, return on investment, and crew share for old and new boats, varying vessel capacity from 70 to 150 tons for old boats and 66 to 264 tons for new boats, the gross revenue from $50,000 to $250,000 in increments of $50,000, and the catch composition from that of the 1967 landings through 100% mackerel, ½ mackerel and ½ anchovies, and 100% anchovies. There are sample calculations and summary tables in Perrin and Noetzel (1970).

The conclusions we reached based on these calculations were pretty much what we expected. For the old boats, we found a dichotomy of interest between the vessel owner and the crew with respect to vessel size. The highest crew share at any level of revenue is with the smallest vessel, whereas the highest profit is with the largest vessel. Crew share is most affected by vessel size, but profit is most affected by composition of the catch.

For example, the maximum effect on profit at $200,000 revenue is about $13,000; this is the difference between an all-anchovy catch and an all-mackerel catch. The best situation, given existing boats, from the standpoint of profit is a 150-ton boat taking an all-mackerel catch. The best from the standpoint of the crew is a 70-ton boat taking a ½-mackerel ½-anchovy catch, by value. The break-even point for a 150-ton old vessel ranges from $65,000 for an all-mackerel catch to about $90,000 for an all-anchovy catch. These amounts are well within the range of gross revenue attained in the past. Because the market value of these old boats is very low, high return on investment can be attained with comparatively low profits. So we concluded that, given favorable market conditions, it would be feasible to expand the fleet under present conditions of catch rates and fish prices, using surplus vessels from other fisheries. This, of course, is saying nothing about stock sizes or availability, or about institutional barriers.

The outlook for new construction is a different matter. The break-even point for the optimum boat with a 50% construction subsidy, and with a catch composition similar to those of the past, is about $150,000, which is close to the upper end of the range of gross revenue in recent years. In order to make a profit comparable to the profit made by top boats in the present fleet (about $30,000), gross revenue of about $225,000 would be required. For an all-anchovy catch, the figure would be closer to $275,000. $275,000 worth of anchovies at $20 per ton is 13,750 tons. For a 100-ton boat, this would mean a full load every 3 days or less on a sustained basis all year, which probably is impossible. We concluded that unless fish prices or catch rates go up considerably, new construction is not advisable, at least under the present share-out system.

The reason for this is the high investment base. A new 100-ton boat would cost about $200,000, while the average market value for the present fleet is only about $50,000. This difference causes very high increases in insurance, depreciation, and interest, even with a subsidy.

If the share-out schedule were revised, things might be different. A 66-ton new boat could make a $20,000 profit, or about 10% return on total capital, with an all-anchovy catch worth $150,000 (about 7,500 tons), if the boat's share of net proceeds were 55%, instead of the 37½% it is now. With a crew of seven, the crew share would be about $8,600.

Looking to the future and the systems approach, we have programmed our costs and earnings model, and it is ready to integrate with a production model, being developed by Dr. Lenarz in our laboratory, and a demand model; so that we can carry out bioeconomic simulation studies of the wetfish industry.

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7140

THE RELATION BETWEEN EXERCISE AND BIOCHEMICAL CHANGES IN RED AND WHITE MUSCLE AND LIVER IN THE JACK MACKEREL, *Trachurus symmetricus*

AUSTIN W. PRITCHARD,[1] JOHN R. HUNTER,[2] AND REUBEN LASKER[2]

ABSTRACT

Glycogen, lactic acid, and fat concentration in red and white muscle and glycogen in the liver of jack mackerel, *Trachurus symmetricus*, were measured after periods of forced swimming by *Trachurus* at speeds above, below, and at the sustained speed threshold. Failure to swim at any speed was associated with an almost complete depletion of glycogen in the white muscle only. The trend of glycogen use in the red muscle closely followed that of the liver and was not correlated with failure to swim. Reduction of glycogen levels in red muscle and liver were associated with extended periods of swim-
Lipid use was slow and not correlated with fatigured muscle and was insignificant in white muscle.
ming. High lipid content was characteristic of e. A decline in lipid concentration after exercise occurred only in the red muscle and only after a swimming period of 6 hr at a subthreshold speed. High lactate levels were characteristic of both muscle types and did not appear to be related to fatigue at any swimming speed.

The high lactate levels in white muscle, the almost complete depletion of glycogen in the white muscle of exhausted fish, and the parallel pattern of glycogen depletion in red muscle and liver suggested that white muscle was the primary locomotor organ near and above the threshold for sustained speed. At these speeds red muscle like the liver may provide nutrients to the white muscle, provided time for mobilization is sufficient. At speeds below the sustained speed threshold our analysis indicated that both the red and white muscle systems were used but the relative significance of the locomotory role played by each system could not be evaluated.

The lateral musculature of many fishes may be readily segregated by color into red and white portions. Typically in active fishes the red muscle makes up from 10 to 20% of the total musculature and is arranged in a thin lateral sheet just beneath the skin whereas the white muscle makes up the underlying mass of the myotome. The two muscle types also differ in the diameter of their muscle fibers, speed of contraction, blood supply, mitochondrial content, patterns of innervation, and glycogen and fat content (Bone, 1966).

The accepted view of the function of red and white muscle tissues in fishes was outlined by Bone (1966). He concluded from his own work on dogfish and from an extensive literature review that the two muscle fibers represent two separate motor systems which operate independently, utilize different metabolites, and serve different locomotory functions, viz., the red muscle is used for slow cruising speeds and functions by aerobic metabolism of fat whereas the white muscle is used for rapid bursts of swimming and is driven by anaerobic glycolysis. Bone's conclusions have subsequently been supported by measurements of oxygen uptake in red and white muscle by Gordon (1968) and by electrophysiological studies on oceanic skipjack, *Katsuwonus pelamis*, by Rayner and Keenan (1967). On the other hand, Braekkan (1956) and Wittenberger (1967) believe the red muscle has no independent locomotor role and functions as a metabolic organ for the white muscle. Electrode recordings from the red muscle (Bone, 1966; Rayner and Keenan, 1967) have provided irrefutable evidence for an independent locomotor function of red muscle at certain slow speeds, but the metabolic independence of the two muscle systems and their metabolic and locomotor function at higher speeds is still open

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to question. Although the roles assigned to the two muscle systems are dependent on swimming speed, no studies have been made on the function of the muscle systems using normally swimming intact animals at known speeds. The objective of this study was to re-examine the metabolic and locomotor roles of red and white muscle by measurement of glycogen, lactate, and fat levels in the muscle and glycogen levels in the liver in fish exposed to various velocity treatments of known strength and duration. Juvenile jack mackerel, *Trachurus symmetricus,* were used in this study because the maximum sustained speed threshold for 6 hr of continuous swimming had already been established for this species (Hunter, 1971), and consequently we were able to relate all of our chemical measurements to known levels of swimming performance.

METHODS AND PROCEDURES

SWIMMING TESTS

Jack mackerel were maintained at a regulated seawater temperature of 18.5° C in a plastic swimming pool 4.57 m diameter and fed an abundant ration of brine shrimp, *Artemia,* and chopped fish and squid each day. The fish were not fed for 20 hr prior to testing. Jack mackerel were tested in an activity chamber patterned after that of Beamish (1968) and described in detail by Hunter and Zweifel (1971). The swimming compartment of the apparatus consisted of a tube 230 cm long and 41 cm in diameter through which seawater could be moved at speeds ranging from 12 to 212 cm/sec. Fish were placed in the tube and forced to swim at a water speed for certain periods varying from 8 min to 6 hr. At the end of the swimming period they were removed and dropped immediately into liquid nitrogen and the frozen fish were stored at —30° C until used for chemical analysis. The time required for removal and freezing did not exceed 1 min.

Speed treatments for the experiments were chosen relative to the 50% endurance threshold for jack mackerel at 22 $L^{0.6}$/sec for 6 hr of swimming where L is total length (Hunter, 1971). Five jack mackerel, mean length 14.6 cm, were tested at the subthreshold speed of 19.6 $L^{0.6}$/sec (98 cm/sec); 14 jack mackerel, mean length 16.3 cm, were tested at the near threshold speed of 21.1 $L^{0.6}$/sec (113 cm/sec); and 10 jack mackerel, mean length 14.7 cm, were tested at the superthreshold speed of 27.7 $L^{0.6}$/sec (139 cm/sec). Fish tested at the subthreshold speed swam continuously for 6 hr and were sampled at the end of that period. Fish tested at the threshold speed were divided into two groups: seven fish that were sampled after 6 hr of continuous swimming; and seven fish that fell from exhaustion at some time during the 6-hr period. The latter group of seven fish were quickly removed from the apparatus and frozen as soon as they fell against the rear screen. Fish tested at the superthreshold speed were also divided into two groups: those that swam successfully for 8 min; and those that failed after 8 or less minutes of swimming.

Ten jack mackerel, mean length 14.5 cm, were used as controls. Five of the control animals were removed from the holding tank, placed in the apparatus, allowed to swim for 30 min at the slow speed of 6.2 $L^{0.6}$/sec (30 cm/sec), removed, and frozen. The other five control fish were removed from the holding tank and immediately frozen. The data from these two control groups were later combined because no difference between them was detected.

CHEMICAL ANALYSES

White and red muscle were dissected from the frozen fish while still frozen. One lateral strip of red muscle was used for fat analysis and the other divided into two equal portions for lactate and glycogen analysis respectively. About 1 g of white muscle from the dorsal portion of the myotome was used for glycogen determinations, 0.5 g for lactate, and 0.5 g for fat measurements. Fish were returned to the freezer and liver samples (0.1-0.2 g) were analyzed for glycogen about a month after the muscle determinations.

For lactate measurements muscle was quickly cut into small pieces, weighed, and homogenized in 10% trichloroacetic acid in prechilled tubes. Proteins and cellular debris were spun down in a clinical centrifuge. Aliquots of the protein-free supernatant fluid were analyzed for lactate enzymatically using the test reagents supplied by SIGMA Chemical Company.[3] The test is based on the conversion of nicotine adenine nucleotide (NAD) to the reduced form (NADH) as lactate is converted to pyruvate by lactate dehydrogenase. All readings were made at 340 mμ on a Beckman DU spectrophotometer. Results are expressed as mg of lactic acid per 100 g wet weight muscle tissue.

Muscle and liver samples for glycogen determinations were dropped into preweighed graduated centrifuge tubes containing 3 ml of 30% potassium hydroxide. Glycogen was precipitated with alcohol and determined according to the method of Montgomery (1957). All readings were made at 490 mμ on a Beckman DU spectrophotometer. Results are expressed as mg glycogen (as glucose) per 100 g wet weight in the case of muscle, and as percent glycogen in the case of liver.

Muscle tissue was dried in an oven at 60° C to constant weight for fat analysis. Fat was removed by a soxhlet extraction with chloroform-methanol (2:1, v:v). After the extraction the solvent in the tissue was evaporated and the difference in weight of the tissue recorded (Krvarić and Mužinić, 1950).

RESULTS

Fish that swam continuously for 6 hr at the subthreshold speed of 98 cm/sec and at the threshold speed showed no difference in the glycogen content of the white muscle from the controls (Table 1). On the other hand, in fish

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[3] P.O. Box 14508, St. Louis, Mo. 63178. Reference to commercial products does not imply endorsement.

TABLE 1.—Glycogen in red and white muscle, and liver of jack mackerel following various forced swimming conditions. Red and white muscle glycogen in mg per 100 g wet weight; liver glycogen is percent of wet weight. -- indicates measurement was lost during analysis.

	Controls			19 $L^{0.6}$ Subthreshold speed			21 $L^{0.0}$ Threshold speed successes		
	Red	White	Liver	Red	White	Liver	Red	White	Liver
	76.6	85.9	6.42	15.23	53.90	0.125	26.71	204.3	0.043
	102.8	--	9.49	52.80	143.2	4.36	33.33	159.4	1.63
	176.3	--	22.74	192.5	76.69	.317	37.59	80.74	1.85
	277.8	276.8	8.75	145.2	316.2	8.31	95.93	492.8	.125
	562.0	142.6	18.59	147.6	102.6	3.16	152.4	223.2	3.42
	706.0	157.9	18.17				191.7	638.0	3.19
	1075	267.8	10.26				475.1	216.3	1.38
	1394	72.9	17.00						
	1417	71.1	11.82						
	1706	216.5	24.24						
Mean	749.4	161.4	14.75	[1]110.7	138.5	[1]3.25	[1]144.7	287.8	[1]1.66

	21 $L^{0.6}$ Threshold speed fatigued			28 $L^{0.6}$ Superthreshold speed-individually fatigued			28 $L^{0.6}$ Superthreshold speed, 8-min test		
	Red	White	Liver	Red	White	Liver	Red	White	Liver
	11.5	26.50	.078	--	--	0.546	--	39.93	10.00
	16.00	4.51	.034	149.6	8.02	4.73	298.6	141.9	10.00
	17.10	20.63	3.30	215.0	19.56	3.83	473.3	25.44	3.16
	40.55	27.77	5.04	490.4	6.76	13.23	533.1	141.0	10.94
	104.8	--	11.96	654.5	18.49	5.81	553.9	57.22	11.31
	151.8	11.15	.820						
	241.5	50.2	12.50						
Mean	[1]83.27	[1]23.46	[1]4.82	377.4	[1]13.21	[1]5.63	464.7	[1]81.1	9.08

[1] Differed from the controls, $P \leqslant 0.05$, Mann Whitney *U* test (Siegel, 1956).

that failed to swim the full 6 hr at the same speed the glycogen levels in the white muscle were lower and were different from the controls ($P = 0.001$ Mann Whitney U test, Siegel, 1956). Glycogen levels in white muscle of all fish tested at the superthreshold velocity were also much lower and statistically different from the controls ($P = 0.05$). The lowest glycogen levels of all were in fish that failed from exhaustion at superthreshold speeds. The values in these exhausted fish were statistically different from those of fish that swam at the same speed but which were removed after 8 min of swimming before they could fall from exhaustion. In sum, strenuous exercise and exhaustion regardless of speed were associated with a marked depletion of glycogen reserves in the white muscle, whereas successful swimming for 6 hr at subthreshold or threshold speed produced no significant change in white muscle glycogen.

The glycogen content of the liver and red muscle were lower and different from the controls in fish tested at threshold and subthreshold speeds ($P = 0.05$). At superthreshold speed, on the other hand, the glycogen content of the red muscle was not different from the controls and that of the liver was different only in fish that failed from exhaustion ($P = 0.02$).

Thus, the trends in the levels of red muscle and liver glycogen in relation to swimming speed were nearly the reverse of that for white muscle glycogen. Low levels of glycogen in red muscle and liver were associated with slow speeds that could be sustained for extended periods. These results suggest that glycogen from red muscle and liver provide energy to the white muscle at nearly all swimming speeds. We believe that no drop occurred in red muscle glycogen in fish fatigued at high speeds because the time was too short for the white muscle to mobilize significant amounts of glycogen. This view is supported by the negative correlation between the level of glycogen in the red muscle and swimming time to fatigue at threshold speed. This is illustrated in the following table:

Threshold speed $= 21\ L^{0.6}$

Time to fatigue (*min*)	Glycogen in red muscle (*mg per* 100 *g wet weight*)
282	11.5
110	16.0
131	17.1
79	40.6
15	104.
38	241.

($r_s = -0.857$, $P < 0.05$)

In fish exercised at the superthreshold speed the lactic acid content of the red and white muscle was considerably above that of the controls and statistically different from them ($P = 0.05$) (Table 2). At threshold and subthreshold speeds, the lactic acid concentration in red and white muscle formed no distinct pattern. At threshold speed the lactate levels of red and white muscle were about the same as the controls and did not differ from them except for one case where the values were actually lower

TABLE 2.—Concentration of lactic acid in red and white muscle of jack mackerel following various forced swimming conditions. Values given are mg lactic acid per 100 g wet weight.

	Controls		19 $L^{0.6}$ Subthreshold speed		21 $L^{0.6}$ Threshold speed successes	
	Red	White	Red	White	Red	White
	40.49	233.0	94.6	520.9	20.60	310.4
	59.29	425.3	97.6	596.6	22.83	344.5
	71.58	387.5	99.2	521.9	26.79	385.3
	77.46	521.0	117.1	630.3	45.66	464.8
	79.53	570.3	156.8	762.3	56.94	403.1
	82.19	341.5			82.19	345.2
	86.76	390.6			83.87	410.2
	86.76	319.0				
	86.76	553.4				
	95.44	589.6				
Mean	76.63	433.1	[1]113.1	606.4	[1]48.41	380.5

	21 $L^{0.6}$ Threshold speed fatigued		28 $L^{0.6}$ Superthreshold speed - individually fatigued		28 $L^{0.6}$ Superthreshold speed, 8-min test	
	Red	White	Red	White	Red	White
	26.23	564.6	101.2	422.9	124.2	724.1
	39.61	545.3	108.4	538.6	132.3	668.9
	56.58	404.4	120.4	723.1	189.0	799.9
	66.6	499.2	151.9	745.8	202.8	807.4
	86.76	489.7	230.5	800.6	237.4	733.5
	122.5	486.2				
	205.5	646.1				
Mean	86.25	519.4	[1]142.5	[1]646.2	[1]177.1	[1]746.8

[1] Differed from the controls, $P \leqslant 0.05$, Mann Whitney U test (Siegel, 1956).

than the controls; at this subthreshold speed lactate levels of red and white muscle were higher than the controls and differed statistically ($P = 0.02$). We have no explanation for these differences except to suggest that the high muscle lactate concentration in the control animals may have obscured changes resulting from moderate exercise. A larger sample size may be required to obtain reliable measurements of differences in lactic acid concentration caused by moderate exercise.

Muscle lactate level did not appear to be related to fatigue at any swimming speed. Lactate levels in fish that fatigued at the threshold speed were not different from the controls. Fish that failed at superthreshold speeds had a higher muscle lactate level than did the controls but the level did not differ from that of fish that swam at the same speed but were removed before they became exhausted. These results suggest that high lactic acid concentration in muscle was not the principal cause of exhaustion.

Red muscle contained considerably more fat per unit weight than white muscle. Indeed, white muscle fat levels were almost undetectable in many cases (Table 3). White muscle fat levels did not differ from the control at any speed level. Red muscle fat did not differ from the controls at threshold and superthreshold speeds but at the subthreshold speed the mean level of fat in the red muscle was lower than the controls and differed statistically from them ($P = 0.02$). Thus only when the fish swam for at least 6 hr at subthreshold speed was there evidence of fat utilization in the red muscle.[4] The reduction in fat in the red muscle suggests that the red muscle system may have been used at the subthreshold velocity. On the other hand, presence of high muscle lactate in both red and white muscle and the drop in red muscle and liver glycogen at subthreshold speeds implies that the white muscle was also active.

TABLE 3.—Fat analyses in red and white muscle of jack mackerel following various forced swimming conditions. Where 0.0% is given for white muscle, only traces of fat were found with the chloroform-methanol extraction. For convenience zeros were used for averaging. Values given as percent dry weight of tissue.

	Controls		19 $L^{0.6}$ Subthreshold speed		21 $L^{0.6}$ Threshold speed successes	
	Red	White	Red	White	Red	White
	20.16	1.98	15.07	0.230	16.91	0.0
	21.00	0.0	15.69	2.12	22.45	0.0
	21.78	.337	16.19	1.24	23.80	2.19
	22.24	1.15	20.54	0.0	24.67	0.0
	23.05	1.32	24.63	0.0	24.97	1.54
	25.11	0.0			26.43	4.09
	25.14	.390			29.37	4.10
	25.89	.924				
	27.29	2.65				
	32.32	2.20				
Mean	24.40	1.10	[1]18.42	.718	24.08	1.70

	21 $L^{0.6}$ Threshold speed fatigued		28 $L^{0.6}$ Superthreshold speed - individually fatigued		28 $L^{0.6}$ Superthreshold speed, 8-min test	
	Red	White	Red	White	Red	White
	21.30	0.0	16.54	0.0	21.96	2.01
	21.97	0.0	16.71	0.0	23.08	.04
	22.47	0.0	26.47	1.22	24.20	.18
	28.70	0.0	28.19	.732	25.57	.50
	30.11	2.56	28.70	2.13	29.54	2.26
	32.08	1.12				
	32.90	6.46				
Mean	27.08	1.45	23.32	.816	24.87	.998

[1] Differed from the controls, $P = 0.02$, Mann Whitney U test (Siegel, 1956).

DISCUSSION

Control levels of jack mackerel white muscle glycogen were similar to those recorded by Canadian workers for mixed red and white muscle in salmonids (Black, Robertson, and Parker, 1961; Black et al., 1962; Connor et al., 1964) and to those from a variety of marine teleosts (Beamish, 1968; Fraser et al., 1966; Wittenberger, 1968; Wittenberger et al., 1969). Red muscle glycogen has not often been separately determined. Our mean control value of 750 mg percent was somewhat higher than the mean of 420 mg percent reported by Wittenberger (1968) for *Trachurus mediterraneus ponticus*, a related species from the Black Sea. Fraser et al. (1966) gave a range of 215 to 279 mg percent for red muscle glycogen of cod, based on analysis of three fish in a relaxed (anesthesized) state. Wittenberger et al. (1969) reported 320 mg percent in a clupeid, *Harengula humeralis*. A much higher level of 1866 mg percent was given by Bone (1966) for dogfish. In most cases, the concentration of glycogen in red muscle was considerably higher than in white muscle.

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[4] In an earlier and preliminary experiment, five smaller jack mackerel, mean length 9.2 cm, swam at the subthreshold speed of 12.7 $L^{0.6}$/sec (48 cm/sec) for 48 hr without failure and we recorded a decrease in the mean fat content of red muscle from 23.7% (range, 20.4-28.4%; $n = 5$) to 18.0% (range, 16.2-20.8%; $n = 5$) ($P < 0.05$).

Liver glycogen controls in jack mackerel were much higher than those reported previously in teleosts. Connor et al. (1964) for example, obtained values of about 1% in chinook and sockeye salmon and steelhead trout, and found that moderate exercise associated with ascending fishways had no effect on liver glycogen levels. Black et al. (1960) reported liver glycogen levels of 0.5-4% in rainbow trout, and Dean and Goodnight (1964) obtained 0.8-3% in four species of warmwater centrachid fishes. Values similar to ours were reported by Wittenberger and Diaciuc (1965) in carp (13.8%) and by Bellamy (1968) in recently fed red piranha (10.3%). Even if a high degree of gluconeogenesis were operative in jack mackerel, it seems unlikely that this could entirely explain the high levels of liver glycogen.

Control levels of glycogen in jack mackerel white muscle appeared to be similar to those in other fishes. However, in the red muscle and especially in the liver, glycogen levels were usually higher than in fishes studied earlier.

The most striking finding of this study was the virtually complete depletion of glycogen in the white muscle of fish that failed from exhaustion. The depletion of glycogen in white muscle occurred in all fish that failed regardless of the speed of swimming or how long they swam. In fish that did not fail at a near threshold speed of 21 $L^{0.6}$/sec (Hunter 1971) the glycogen in the white muscle did not differ from controls, whereas in the fish that failed, glycogen in the white muscle was at nearly the same low level as it was in fish that failed after a few minutes of exertion at a much higher speed. Red muscle glycogen was also depleted at some swimming speeds but the pattern of glycogen depletion in red muscle closely paralleled that of the liver. Red muscle had one-fifth the lactate found in white muscle on a percent basis but only about one-fiftieth on an absolute basis because the mass of white muscle exceeds the red by 10 to 1.

The high lactate levels in the white muscle, the almost complete depletion of glycogen in the white muscle of exhausted fish, and the parallel pattern of glycogen depletion in red muscle and liver all point to the same hypothesis. In jack mackerel at threshold and higher speeds the energy used for swimming was derived primarily from glycolysis in the white muscle which was the principal locomotor organ. Red muscle like the liver may serve as a storage organ whose resources could be used to drive the white muscle, given sufficient time for mobilization. Thus at threshold speeds, red muscle function appeared to be tied to that of the white and it could not be considered as acting independently. No change in red muscle glycogen was detected at the highest test speed, possibly because time was insufficient to mobilize the glycogen reserves other than in the white muscle itself. This time dependency for mobilizing red muscle glycogen under conditions of strenuous exercise could explain why Bone (1966), Wittenberger and Diacuic (1965), Wittenberger (1968), and Fraser et al. (1966) detected no change in red muscle glycogen after strenuous exercise. It must be remembered that in all of these previous studies the strength and the duration of the exercise was unknown, except that it was considered to be extreme.

The decrease in fat content plus the high lactate levels suggest that the red muscle was used for swimming at subthreshold speeds. Bilinski (1969) showed that the rate of oxidation of fatty acids in red muscle of rainbow trout and sockeye salmon exceeded that in the white muscle by one or more orders of magnitude depending on the fatty acid substrate. On the other hand, neither the high oxidative capacity nor the decline in lipid levels in red muscle with moderate exercise are sufficient evidence for an independent locomotor role. In addition, the presence of high lactate levels in white muscle and the drop in the glycogen content of the white muscle indicated that the white muscle was also used at the subthreshold speed of 19 $L^{0.6}$/sec. The electrophysiological evidence for independent locomotor activity of the red muscle cannot be ignored. At some speed slower than any used in the present experiment jack mackerel may depend only on red muscle for propulsion and on lipids for fuel. At what velocity red muscle begins to play a major role or how significant this speed may be in the life of the animal are questions that remain to be answered. The most tenable explanation for these data is that both muscle systems were used at the subthreshold speed but we are unable to choose which system played the more significant role.

Jack mackerel appear to be specialized in body form and swimming capabilities for high-speed continuous swimming (Hunter, 1971). Thus the physiological characteristics we have described, namely use of glycolysis in white muscle for swimming, high liver glycogen levels, and tolerance of high muscle lactate levels may represent specializations for high-speed swimming and may not be representative of the general pattern in fishes. On the other hand, *Trachurus* may share these characteristics with other fishes of similar habits, for example other carangids and the scombroid fishes. It seems possible that evolution may have favored the development of these physiological characteristics because severe velocity limits may be set by aerobic lipid metabolism.

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7141

THE ACANTHURID FISH *NASO LOPEZI* HERRE FROM THE HAWAIIAN ISLANDS.—Four specimens of *Naso lopezi*, heretofore unknown from the Hawaiian Islands, were taken with a 41 ft shrimp trawl by the Bureau of Commercial Fisheries' R/V Townsend Cromwell during cruise 40 at Sta. 126. This station, one of 10 in the same general area and depth, was occupied at 2100 hr, 2 December 1968 off Haleiwa on the north coast of Oahu (lat. 21° 40′ N, long. 158° 07′ W) at a depth of 55 fms. The bottom temperature was about 25° C. The bottom type in this area was primarily muddy sand, but there were patches of broken shell, calcareous rubble, and live sponges. Station 126 was unusually rich in sponges, and it was also the most productive in fishes, with 33 species being captured. The dominant fishes were *Trachinocephalus myops*, *Pristipomoides microlepis*, *Dactylopterus orientalis*, *Lagocephalus hypselogeneion*, *Parupeneus chrysonemus*, and *Priacanthus* spp.

N. lopezi was described by Herre (1927: 467–468, pl. 7, fig. 2) from four specimens 156–386 mm TL from the Philippine Islands. Fowler and Bean (1929:282–283, fig. 22) recorded another specimen from the Philippines; however, they identified their fish as *Naso vomer* (Klunzinger) and placed *N. lopezi* in the synonymy of *vomer*. Myers (1940) corrected their error. Smith (1966), who reviewed the subfamily Nasinae, agreed with Myers on the validity of *lopezi* and provided additional descriptive information (from Myers) on three Philippine specimens, 420–480 mm FL, from the collection of Stanford University.

Tomiyama and Abe (1958: 123, fig. 362) recorded the species from Japan [as *Callicanthus hexacanthus* (Bleeker)]. They stated that it occurs in their country only as young.

TABLE 1. MEASUREMENTS OF SPECIMENS OF *Naso lopezi* FROM HAWAII EXPRESSED AS PERCENT OF STANDARD LENGTH.

SL (mm)	Depth of Body	Head Length	Eye Diam.	Caudal Fin	1st Dorsal Spine
435	37.1	24.2	4.9	17.8	8.7
273	38.5	25.1	7.1	21.6	10.7
134	42.8	26.9	8.9	21.6	12.7
97.5	44.4	27.8	11.6	22.1	12.2

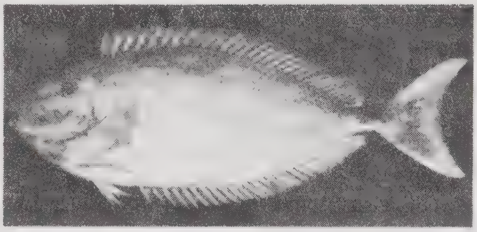

Fig. 1. *Naso lopezi*, USNM 204941, 435 mm SL, Oahu, Hawaiian Islands.

The four Hawaiian specimens are 435, 273, 134, and 97.5 mm in standard length; the largest and smallest have been deposited in the U. S. National Museum (USNM 204941) and the remaining two in the Bernice P. Bishop Museum (BPBM 9177).

Meristic data from the Hawaiian specimens are as follows: D VI,26 to 28; A II,27; P_1 16 to 18; P_2 I,3; gill rakers 4 + 1 + 9 or 10. Dorsal and anal fin ray counts from western Pacific specimens, collectively, are D V or VI,26 to 31; A II,27 to 30. Only the Fowler and Bean specimen and Japanese specimens are listed with VI dorsal spines.

The teeth are narrow and lanceolate with about six tiny serrations on each upper lateral edge. Many teeth are missing from the jaws of the specimens; the counts range from about 40 upper and 36 lower teeth in the smallest fish to about 70 upper and 65 lower teeth in the largest.

Fixed caudal plates, so characteristic of the genus, vary from about 1% of the standard length of the two smaller specimens, with the lateral keel a mere nubbin, to about 4% in the two larger specimens, with a hemispherical keel which extends laterally up to one-third the length of the basal plate.

Some of the body and fin proportions are relatively constant. For example, the body width is about 14% of the standard length; the least depth of the caudal peduncle is 4% to 5% of the standard length; and the length of the pectoral fins ranges from 15.2% to 17.9% of the standard length. Other measurements display more variation, most of which seems to be a function of increasing size (Table 1).

In terms of standard length, the snout seems unchanging, varying randomly among the four specimens from 15.1% to 15.9% SL; however, as is apparent from a comparison of Figs. 1 and 2, both the body and the snout become more elongate with age. The change in snout proportions is somewhat more evident when compared to head length; the snout is 5.5% of the head length in the smallest specimen and 6.3% in the largest.

Color in preservative is brownish gray with numerous small dark brown spots or short lines on the body, caudal fin, and a few on the head; there is a nearly continuous narrow dark brown band following the lateral line.

Two other species of *Naso*, *N. tuberosus* (Lacépède) and *N. fageni* Morrow, have small dark spots; however, both, as adults, display a prominent rostral prominence (though not a horn as in *unicornis* and other species) which is entirely lacking in *lopezi* even in the largest adults.

This record of *N. lopezi* brings to six the number of species of *Naso* known from Hawaii. As pointed out by Randall (in Gosline and Brock, 1965), one of these, *Naso annulatus*, is recorded from only a single specimen [the type of *Naso incipiens* (Jenkins)].

If the only record of *N. lopezi* from Oceania were Hawaii, this distribution would not be unusual. On checking the literature we find 28 fishes which are known only from Hawaii and the western Pacific, and another 10 extend their range into the Indian Ocean. Nearly all of these are species from moderate to deep water.

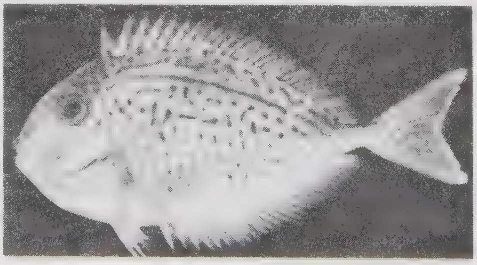

Fig. 2. *Naso lopezi*, BPBM 9177, 134 mm SL, Oahu, Hawaiian Islands.

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7142

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On the influence of the Norwegian–Greenland and Weddell seas upon the bottom waters of the Indian and Pacific oceans*

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Abstract—The bottom waters of the North Pacific and North Indian oceans have temperature and salinity distributions that suggest origins from the extreme waters of the Norwegian–Greenland and Weddell seas. We attempt to trace these waters from their sources to the abyssal Pacific and Indian oceans by examining distributions of temperature and salinity along a stratum defined by density parameters. We assume that the major flow and mixing will take place along such surfaces, though the results make plain that vertical mixing is also important. The density stratum we have chosen to examine extends from the sea surface in the Norwegian–Greenland Sea and from near the surface in the Weddell Sea to depths of about 3500 m in the central oceans and below 4000 m in the North Pacific.

The cold and saline water of the Norwegian–Greenland Sea is traced along the density stratum through the Denmark Strait, where vertical mixing raises both temperature and salinity to their maximum values in the central North Atlantic. From there the temperature and salinity decrease monotonically southward toward the Weddell Sea, partly by lateral mixing with the cold, low-salinity waters on this stratum where it lies near the sea surface in the Weddell Sea, and partly by vertical mixing with the underlying Antarctic Bottom Water. From the southern South Atlantic the high values of temperature and salinity (the stratum now lies close to the vertical maximum in salinity) extend eastward with the Antarctic Circumpolar Current into the Indian and Pacific oceans, with monotonically decreasing temperature and salinity as further vertical mixing erodes the maximum in salinity, until the salinity maximum is found at the bottom in the North Pacific Ocean.

The stratum we have defined terminates at abyssal depths in the northern Indian and Pacific oceans; since water must rise somewhere to balance the sinking in regions of bottom-water formation, there must be upward flow across the stratum elsewhere. The tremendous areal extent of the salinity maximum, however, suggests that the upward flow through the stratum must be minimal except in the North Indian and North Pacific oceans, where stability is shown to be very low at the depth of the stratum.

PURPOSE

THE PURPOSE of this study is to examine the relation of the bottom waters of the North Pacific and North Indian oceans to the various supposed sources of deep water in the World Ocean. Earlier studies (WÜST, 1929, 1938, 1951; SVERDRUP, 1931; COCHRANE, 1958; MONTGOMERY, 1958; POLLAK, 1958; STOMMEL and ARONS, 1960; BOLIN and STOMMEL, 1961; MUNK, 1966) have examined the problem through simple distributions of temperature, salinity, and oxygen, through budgets of such characteristics and through mathematical models based more or less on the distribution of such characteristics.

One characteristic that has not been used explicitly in such studies is density. There are obvious difficulties both in defining such a parameter and in making valid interpretations. Although density parameters have been used to illustrate oceanic features and to obtain interesting and useful results (MONTGOMERY, 1938; TAFT, 1963; KUKSA, 1963; REID, 1965; CANNON, 1966; BARKLEY, 1968; TSUCHIYA, 1968; RUPP, 1969), they have mostly been limited to the use of potential density in the upper layers (0–1500 m). At greater depths potential density may have inversions (WÜST, 1933; KAWAI, 1966; LYNN and REID, 1968) and therefore cannot be taken to represent surfaces of flow or mixing. We have attempted to use a method that may allow us to use density parameters, in at least an approximate fashion, over a wider range of depth (pressure), and to investigate the deep and abyssal waters on the usual assumptions of isopycnal flow and mixing.

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METHOD

LYNN and REID (1968) have suggested that the usefulness of isopycnal analysis may be extended to deep waters by calculating density referred to an appropriate pressure; and that, where water masses and density surfaces extend through wide depth ranges, mixing paths may be constructed of short segments of such density surfaces, each referred to appropriate pressures. It is not immediately clear that this method can yield useful results; therefore, some of the concepts are reviewed below.

Isopycnal analysis

Isopycnal surfaces (referred to a sea pressure of zero decibars) have frequently been used to investigate lateral mixing and circulation in the ocean. The assumption is made that exchange can take place more readily along isopycnal surfaces than across them, since such exchange does not significantly alter the field of density, and little work need be done to effect the exchange. Vertical mixing must be assumed either to be negligible or to take place in such a fashion that a parcel must mix with both deeper and shallower layers so that its own density is not changed by the mixing, though its other characteristics may be. The latter assumption is particularly awkward if one is dealing with water near the bottom.

The effect of pressure on mixing

Pressure has been assumed constant in such studies. Although the various assumptions are not entirely fulfilled, the method has been useful in studies of mixing and circulation in the upper few hundred meters. Even at shallow depths the pressure variation can be troublesome, but, when mixing and flow through the entire depth range of the ocean are considered, the pressure effects are so severe that they cannot be ignored.

An ordinary θ–S diagram (potential temperature versus salinity) is shown in Fig. 1a with isopycnals drawn corresponding to zero decibars of sea pressure. Figs. 1b and 1c are similar θ–S diagrams, but the isopycnals are drawn for pressures of 2000 and 4000 decibars. They allow one to find the *in situ* density a water parcel would attain if moved adiabatically to depths where the pressure is 2000 or 4000 decibars. The density increases substantially, of course, but the critical difference is that it does not increase uniformly: the slopes of the isopycnals decrease with increasing pressure. This is mostly the effect of the variation of compressibility with temperature: the colder water is more compressible.

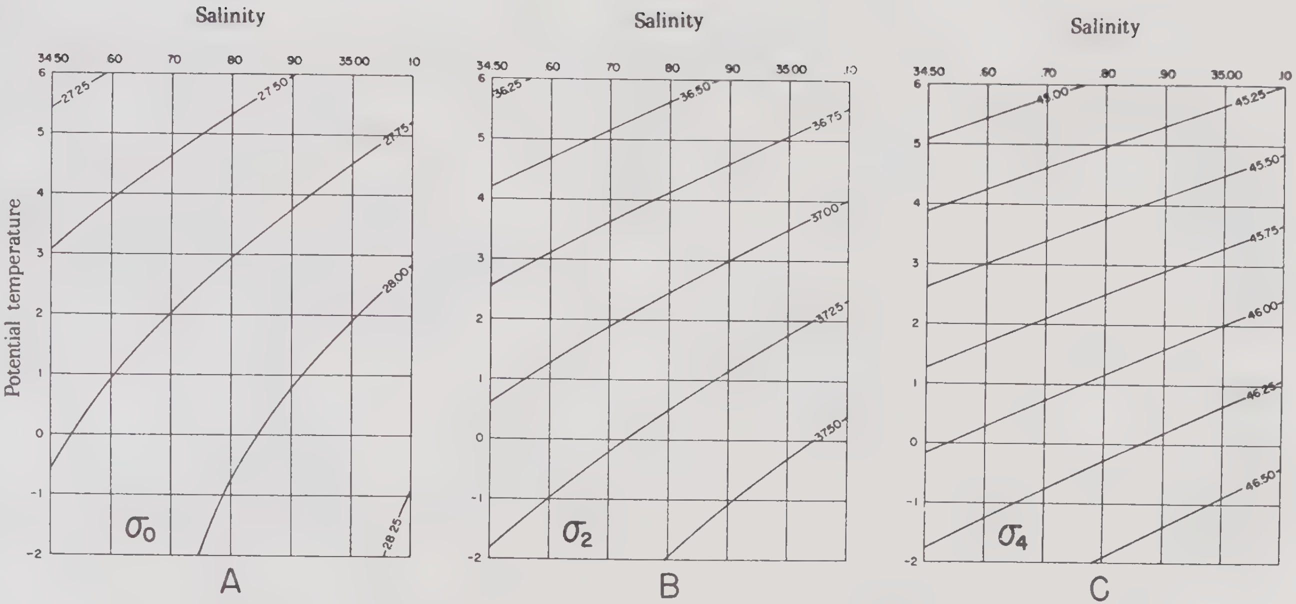

Fig. 1. Density at sea-surface pressure (σ_0), at 2000 decibars pressure (σ_2) and at 4000 decibar^{S} pressure (σ_4) as functions of salinity and potential temperature.

One simple interpretation of such diagrams is that a water sample, whose characteristics are θ, S, and p (pressure), can be more usefully represented on a θ–S diagram if a segment of the isopycnal appropriate to its *in situ* pressure is drawn through the point. Under the original assumptions, mixing will occur most freely with those other water parcels which lie adjacent to it along the same isopycnal, so long as the pressure does not vary. If a water parcel moves to a different depth, the slope and value of the isopycnal segment will change and it should mix with water parcels along a different curve.

However, this does not lead to a uniquely determined set of lines or surfaces along which all water parcels are miscible under the desired criterion of no change in the density field, or a minimum of work. This can be demonstrated in a simple way by considering the following exchanges.

Extreme examples

Consider a water parcel at the sea surface with $\theta = 2°\text{C}$ and $S = 34{\cdot}95‰$. Its σ_0 (or density* determined from its potential temperature and salinity at zero decibars sea pressure; this has been called potential density† and its usual symbol is σ_θ) is about 27·95. If this parcel is moved adiabatically to a depth where the pressure is 4000 decibars, its density (in σ notation, here called σ_4) will be about 45·96. If it mixes at this pressure along the 45·96 isopycnal and achieves a θ of 0·93°C and an S of 34·70‰, and is then moved adiabatically back to the sea surface, its density (σ_0) will be about 27·83. The net change through the adiabatic and lateral paths has been from a σ_0 of 27·95 to a σ_0 of 27·83. Lateral (isopycnal) mixing at one depth (pressure) has thus changed the *in situ* density that the parcel would have at another depth (pressure). If the lateral mixing with cooler, less saline water had taken place at the sea surface, and then the parcel had been moved adiabatically to 4000 decibars, the σ_4 would have been greater than 45·96. Thus it seems impossible to consider lateral mixing without taking into account the pressure at which the mixing occurs. There is no reason to think that exchanges of this sort may not occur in the ocean: a water stratum may be formed near the sea surface with a particular *in situ* density, sink to another pressure, mix laterally, and rise again in another area, arriving at its original pressure level with an *in situ* density different from its original value. (All of this may take place without violating any of the assumptions about lateral mixing.) Conversely, surface waters with different potential densities may freely (without violating these assumptions) mix with (or supply) the same deep-water density stratum.

However, the extreme example given above is not from the real ocean. There are only a few restricted areas where water sinks to great depths, and the temperature and salinity values it encounters there are not so widely different from its own. It thus seems worthwhile to investigate whether the actual circumstances of the ocean are such that the formation and flow of the major water masses can usefully be studied by

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*The density parameter we use is actually $\sigma = 10^3 (\rho - 1)$ where ρ is specific gravity, not density. Density in g/cm^3 is slightly greater than ρ, but we shall use ‘density’ instead of ‘specific gravity’ for brevity of expression and to remain compatible with earlier usage.

†We use the ordinary definitions of ‘potential density’ and ‘potential temperature’ (attained after moving the parcel adiabatically to the sea surface), though they might be generalized to refer to any pressure (i.e. 4000 db, as RUPP (1969) has done).

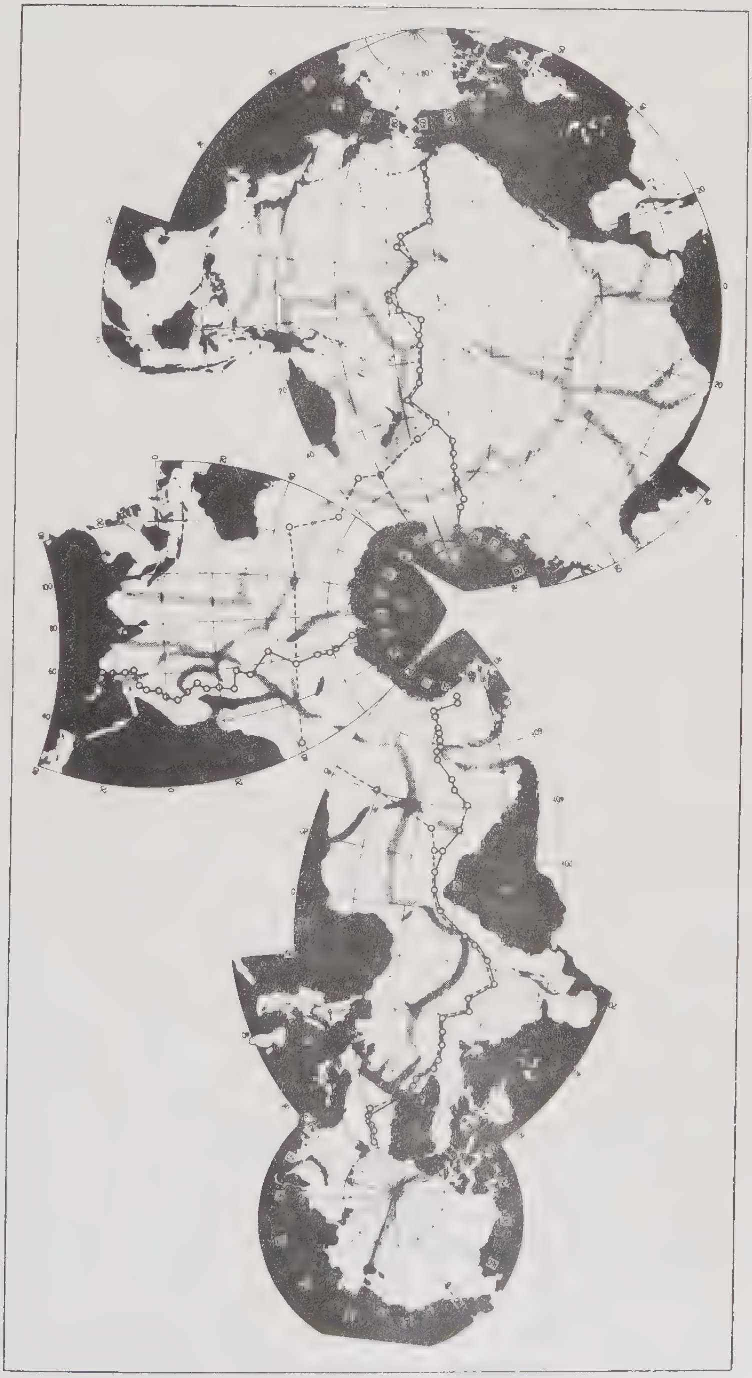

Fig. 2. Positions of the meridional vertical sections shown in Figs. 3a, 3b, 3c and 9. Darkened areas represent the major elevations separating the principal basins.

consideration of exchanges along isopycnal surfaces in which the density is referred to appropriate pressures.

Application of the method

In this exploratory study we have used θ–S diagrams at only three pressures (0, 2000 and 4000 decibars) in following the water, but through examination of the data we conclude that closer spacing would not have significantly altered these results.

We take the surface defined by the density parameters we have chosen as representing a stratum of water of finite thickness. For example, the temperature–salinity characteristics that will be seen along this surface at depths greater than 3000 m fall into only five of the temperature–salinity classes (0·5°C by 0·10‰) whose volumes were calculated by MONTGOMERY (1958) for the World Ocean, but these five classes account for about one-quarter of the ocean volume. Our surface thus can be taken to represent a substantial part of the ocean, and we prefer to refer to it as a stratum.

THE CHOICE OF THE STRATUM

We have chosen to examine a stratum that lies within the layer of high salinity that extends continuously from the North Atlantic to the abyssal Indian and Pacific oceans. SVERDRUP (1931) and WÜST (1951) have discussed this layer, and STOMMEL and ARONS (1960) have based one of their models upon its continuity. In the Indian and Pacific oceans the abyssal water has σ_4 values near 45·92, and this value is found also in the deep waters of the North Atlantic. The continuity of this water mass is clear not only from the distribution of salinity but also from that of σ_0: this density is found at or near the σ_0 maximum* that extends above the bottom in the western Atlantic from about 45°N to 32°S, and beyond there it is either beneath or within the principal salinity maximum of the deep water.

We use this parameter to define the stratum at depths below 3000 m. Where the stratum rises above this depth (in high latitudes), density parameters referred to lower pressures are chosen to define the stratum.

The stratum chosen extends to the sea surface in the Norwegian–Greenland and Barents seas and in the Weddell Sea near the ice shelf, corresponds closely to the salinity maximum of the Antarctic Circumpolar Water and southern Indian and Pacific oceans, and illustrates most of the deepest waters of the Indian and North Pacific oceans. The whole is intended to illustrate the general circulation of a substantial part of the ocean and the nature of the flow and exchanges that take place along this stratum between waters whose extreme characteristics are formed and maintained at distant sources.

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*LYNN and REID (1968) suggested that the σ_0 maximum lay along about $\sigma_4 = 45{\cdot}93$; we have used 45·92, which also closely follows the σ_0 maximum, because it is better defined by the available data in the abyssal Indian and Pacific Oceans.

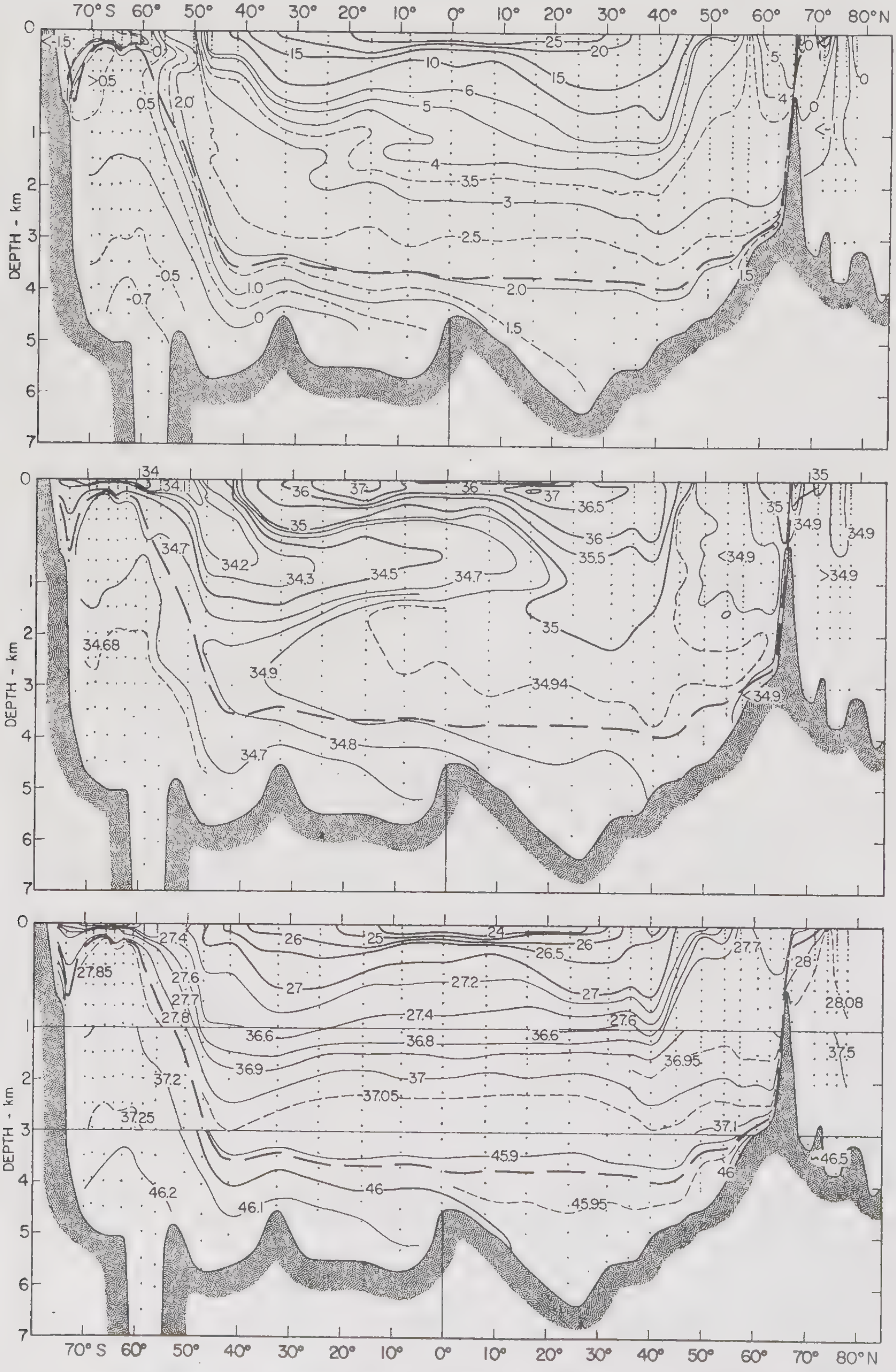

Fig. 3a. Potential temperature, salinity, and σ_0 (0–1000 m), σ_2 (1000–3000 m), and σ_4 (> 3000 m) on a meridional vertical section in the western Atlantic Ocean. On Figs. 3a, 3b, 3c and 11 the vertical exaggeration is $2{\cdot}22 \times 10^3$ above 1000 m depth and $1{\cdot}11 \times 10^3$ below. The heavy dashed line indicates the stratum defined in the text. Stations are identified in the Appendix.

THE LOWER NORTH ATLANTIC DEEP WATER

In the North Atlantic

In describing the waters of the North Atlantic Ocean WÜST (1935) identified two warm, highly saline layers as Upper and Middle North Atlantic Deep Water. Beneath these layers but distinct from the Bottom Water lies a cooler, less saline layer which he called the Lower North Atlantic Deep Water (LNADW). He noted (1933) that this water has a higher potential density than the waters above and below but regarded this as an artifact of errors in the constants used in calculations. In fact, a proper calculation (SCHUBERT, 1935) shows stability despite the σ_0 maximum.

In the North Atlantic south of 50°N (Figs. 2 and 3a) this water lies beneath the warm saline layer and above the cold, less saline water at the bottom. It could not have been formed from a vertical mixture of these two layers, however: it is either colder or more saline than any possible mixture of these layers. It does, therefore, represent a stratum with distinct characteristics (one of which is a potential-density maximum) which must have a distinct origin. We believe that this origin is at the overflow area from the Norwegian–Greenland Sea into the western North Atlantic, and principally in the area between Greenland and Iceland.

The depth where σ_4 equals 45·92 is greater than 3000 m in low and middle latitudes (Figs. 3a, 3b, 3c). Where the surface of σ_4 equal to 45·92 rises to 3000 decibars, we desire to change to a surface defined by a value (or values) of σ_2. If the range of θ and S along the intersection is too broad, then there will be a range of isopycnals (of σ_2, for example) which may be too broad for any single value to be representative. The intersection of the 3000 m surface with the surface where σ_4 equals 45·92 in the North Atlantic occurs only west of the Mid-Atlantic Ridge and in latitudes 47°–63°N, just south of Greenland (Fig. 4a). The length of the intersection is about 2700 km. The θ–S range of the intersection (Fig. 4b) is from 2·04°C, 34·904‰ to 2·12°C, 34·925‰. This range of θ–S, when plotted on a θ–S diagram with isopycnals for 2000 decibars, covers a range of σ_2 from about 37·135 to 37·140. We feel that this range is sufficiently small to justify choosing a single σ_2 value of 37·14 to examine the stratum at depths above 3000 m.

The stratum continues to rise northward beyond the 3000 m level. It intersects the 1000 m surface in the Denmark Strait where at that depth the Strait is no more than 50 km wide (near 65·5°N and 30·5°W). Data are sparse in the region of the intersection and it is not possible to make a good estimate of the θ–S range. Interpolation between stations gives 1·95°C and 34·885‰. A σ_0 value of 27·905 has been chosen, although at this shallower level the range may not be as narrow as at the first transition. The stratum is continuous through the Denmark Straits and extends throughout parts of the Norwegian, Greenland, Barents and Arctic seas at 600 m or less.

Along the stratum that we have defined (Figs. 4a, 4b), the salinity (and temperature) decreases northward through the Denmark Strait, although a wide range of values, including warmer and more saline water, is found in the eastern parts of the Norwegian and Greenland seas. In the Greenland Sea (on the surface where σ_0 equals 27·905) the temperature and salinity range from −0·65°C, 34·68‰ to 3·10°C, 35·01‰, though most of the values are below 1°C and 34·80‰. In the Norwegian Sea the values at 27·905 range from 2·00°C, 34·89‰ to 4·10°C, 35·14‰: part of this warm saline water is flowing northward past Spitzbergen into the Arctic Ocean and eastward

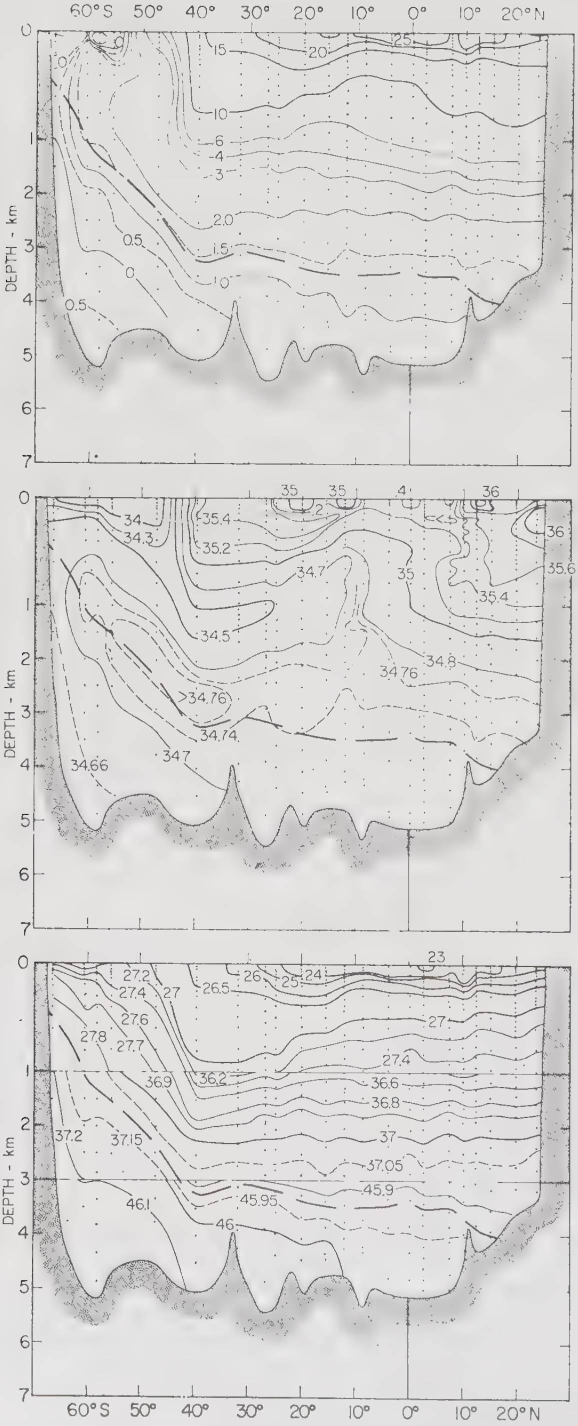

Fig. 3b. Potential temperature, salinity, and σ_0 (0–1000 m), σ_2 (1000–3000 m), and σ_4 (> 3000 m) on a meridional vertical section in the western Indian Ocean. The heavy dashed line indicates the stratum defined in the text. Stations are identified in the Appendix.

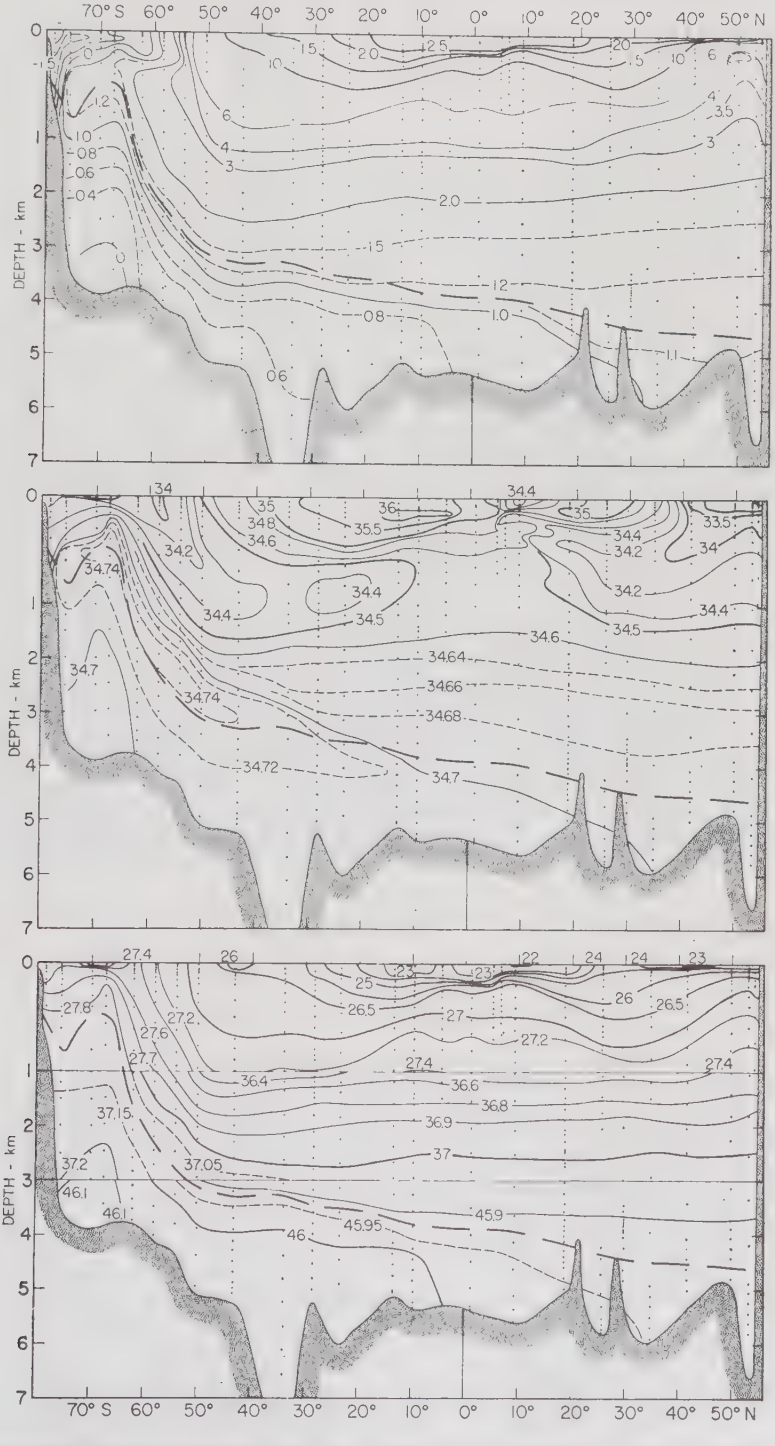

Fig. 3c. Potential temperature, salinity, and σ_0 (0–1000 m), σ_2 (1000–3000 m), and σ_4 (> 3000 m) on a meridional vertical section in the western South Pacific and central North Pacific Ocean. The heavy dashed line indicates the stratum defined in the text. Stations are identified in the Appendix.

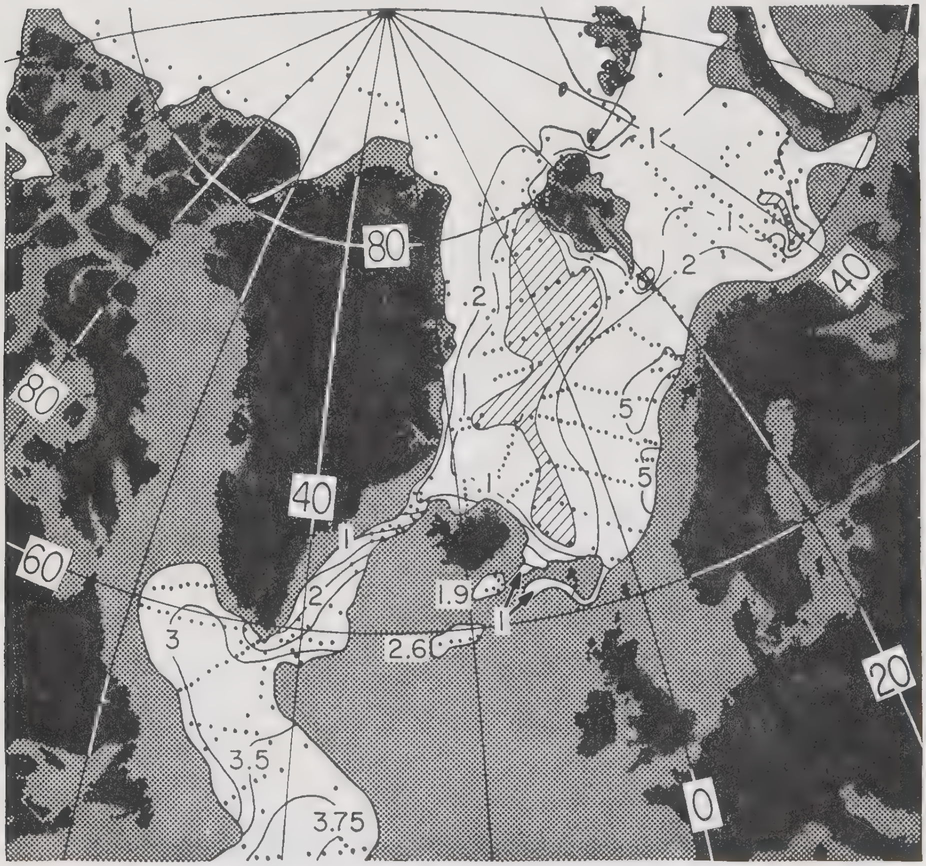

Fig. 4a. Depth (in km) of the stratum where σ_0 equals 27·905 above 1 km, σ_2 equals 37·14 between 1 and 3 km and σ_4 equals 45·92 below 3 km in the northern North Atlantic Ocean and the Norwegian and Greenland seas. Station positions in the Faroe–Shetland Channel are omitted from the figure. Shading indicates areas where the entire column is less dense than this stratum; the area in the Norwegian–Greenland Sea where the entire water column is more dense than this stratum is indicated by hatching. Data are identified in the Appendix.

into the Barents Sea. In addition, north of 62°N this warmer water is separated from the other water of this density in the Greenland Sea: an area near Mohns Ridge contains (at least in winter) no water of σ_0 as low as 27·905. The areal separation and the difference in direction of flow (Norwegian Current flowing north for the warm water, East Greenland Current flowing south for the colder water) suggest that it is the colder waters near Greenland (mostly below 1°C and 34·80‰) that are most available to contribute to the Lower North Atlantic Deep Water if it is to be formed in the Denmark Strait. However, these waters must be made both warmer and more saline to reach the values of 2·12°C, 34·925‰ and σ_2 equal to 37·14 encountered south of the Strait at the 3000 m level.

We cannot clearly establish continuity along the stratum from the high θ and S in the Norwegian–Greenland Sea to the other high values south of Greenland (Fig. 4b).

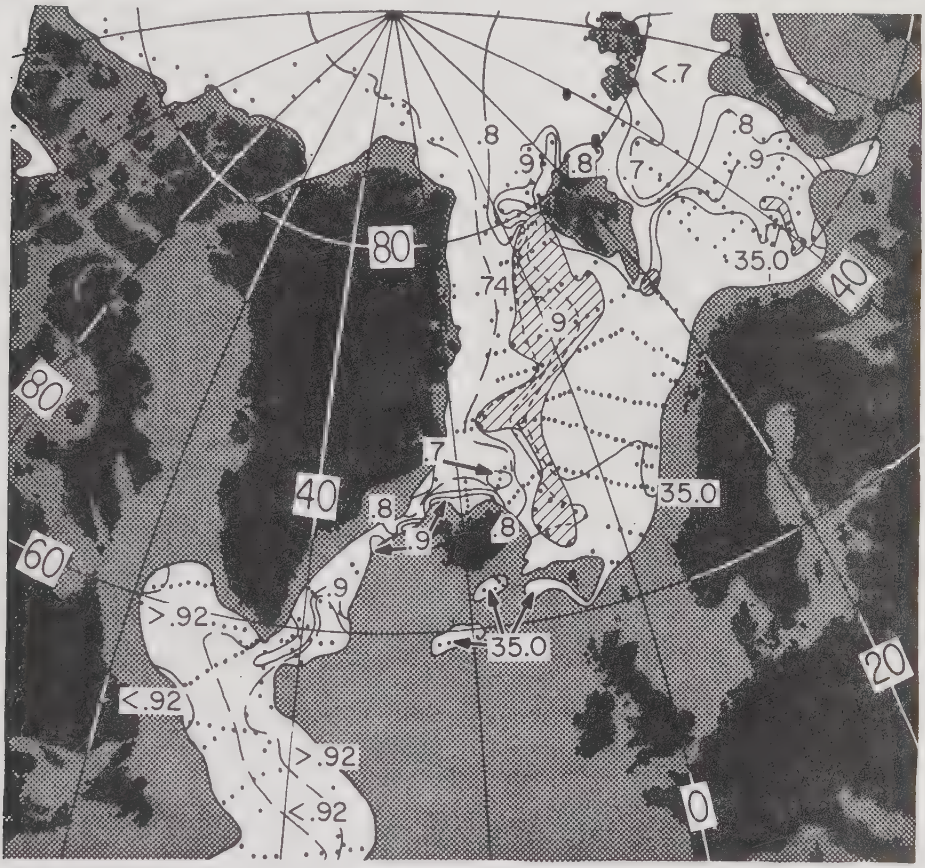

Fig. 4b. Salinity (per mille) along the stratum whose depth is shown in Fig. 4a. The first two digits have been omitted where the salinity value is between 34·0 and 35·0‰.

We therefore seek to account for the latter values by vertical mixing. Some of the warm and saline waters of the Norwegian–Greenland Sea flow southward over the sill east of Iceland along the Reykjanes Ridge, and then turn westward and northward toward the Denmark Strait. This sort of flow has been demonstrated by WORTHINGTON and VOLKMANN (1965) for water of 3·2°C (somewhat shallower than the stratum we have defined). TAIT, LEE, STEFÁNSSON and HERMANN (1967) show that relatively warm and saline water crosses the Iceland–Faroe–Shetland Ridge and lies at depths near 1500 m at the foot of the Ridge; our stratum lies within this water, which is presumably a mixture of Norwegian Sea water with the warmer water south of the Ridge.

CREASE (1965) has shown water of σ_t as great as 28·05 within the Faroe–Shetland Channel. STEELE, BARRETT and WORTHINGTON (1962) find water with σ_t as high as 27·96 (or σ_0 about 27·98) at depths of 2000 m on the slope southeast of Iceland. They calculate this to be Norwegian–Greenland Sea water mixed with warmer water from the south in about equal parts, which flows southwestward past Iceland. However, these high values of σ_0 (27·98) do not appear to be continuous across the Reykjanes Ridge: the water that does cross appears to be less dense.

LEE and ELLETT (1965 and 1967) have investigated the distribution of the Northeast Atlantic Deep Water and pointed out that it crosses the Mid-Atlantic Ridge south of Iceland and extends throughout the northwestern basin. In this basin the Northeast Atlantic Deep Water includes a salinity maximum at a potential temperature of about 3·0°C; on *Gauss* Sta. 222 the θ and S at 2980 m are about 3·0°C and 34·97‰: the σ_2 of this water is 37·05. This is about the densest water that crosses the Ridge, and, after it has crossed, it lies above the water of σ_2 equal to 37·14 which has passed through the Denmark Strait.

Since we are dealing with a density stratum that has a wide depth range, it is more convenient to illustrate this flow by using a density parameter (in this case σ_2) instead of depth as the ordinate in Fig. 5* and to represent depth in the same manner as θ and S. Isobaths and bottom depths are shown at the appropriate σ_2 values. Along 59°30′N, water of our stratum (here at σ_2 equals 37·14) is seen east of the Reykjanes Ridge with salinity as great as 35‰ and θ above 2·5°C. This water has come southward east of Iceland. The highest values of salinity at the bottom occur here and as the water continues to move south, without another source of such saline water, the salinity and density both decrease by vertical mixing. At 53°30′N no values of σ_2 as great as 37·14 are found east of the Ridge, and only a small remnant of the bottom water (against the Ridge) is still above 35‰. South of 53°30′N the water moves westward across the Ridge (where the sill depth is greater) and turns northward again on the west side of the Ridge.

The colder, less saline, but denser waters at 59°30′N from the Greenland Sea have passed southward through the Denmark Strait; they pass southward west of the Ridge beneath the warmer, more saline and less dense waters from the eastern side that are now flowing northward. The vertical mixing that has taken place has cooled and freshened the Iceland–Scotland overflow water and made the Denmark Strait overflow water warmer and more saline. In particular, vertical mixing of waters above and below the stratum has produced waters at the surface where σ_2 equals 37·14 that are more saline and warmer than are found at this density in the Denmark Strait. Characteristics on the stratum have been raised from values of about 2·0°C and 34·89‰ at 59°30′N to values as high as 2·1°C and 34·93‰ at 53°30′N; some observations near this section show salinity as high as 34·94‰ where σ_2 equals 37·14. The lateral maxima in salinity and potential temperature on this stratum in the northwestern Atlantic thus appear to be the product of vertical mixing (at depths of 2·5–3·5 km) of two water masses from shallower levels in the Norwegian and Greenland seas.

Western Atlantic

South of 50°N the depth of this stratum (Fig. 6) on the western side of the Mid-Atlantic Ridge is near 3800 m as far as the equator, except along the coast of North America, where it slopes upward to about 3200 m. The variation of salinity and potential temperature* is very slight in the North Atlantic south of 40°N, and the tongue of saline, warm water (Figs. 7 and 8) is not defined south of about 35°N. The water there is nearly homogeneous in the lateral sense, and, unlike WÜST's (1933) description of the overlying Upper and Middle North Atlantic Deep Water, we cannot claim evidence of a stronger extension along the western boundary.

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*WORTHINGTON and WRIGHT (1970) have used depth as the ordinate in their illustrations of these data and others in the immediate region. MANN, GRANT and FOOTE (1965) and GRANT (1968) also present atlases in which the pertinent details of the temperature and salinity structure in this area can be examined.

The extreme values in the northern part of the western basin are modified gradually toward the south, and the gradients increase. The sharpest increase occurs south of 30°S, probably because of the restriction imposed by the Rio Grande Rise and the Walvis Ridge. South of 40°S the stratum slopes upward again and the Mid-Atlantic Ridge is no longer a major obstacle to exchange between the western and eastern basins.

Eastern basins

High values of S and θ are seen also on the eastern side of the Mid-Atlantic Ridge (Figs. 7 and 8). They reflect the influence of the overlying more saline waters, though the depth of 4600–5000 m is much too great and the temperature (θ) of 2·06°C much too low to be accounted for by direct Mediterranean influence: more likely they also represent the influence of the overflow from the Iceland–Scotland area. The great depth of the stratum in the eastern basins is related to the generally less dense waters found there: only limited amounts of cold Antarctic Bottom Water cross the Ridge through the Romanche Trench. METCALF, HEEZEN and STALCUP (1964) estimate that the controlling depth is about 3750 m, which is within 100 m of our density surface in the area of the Romanche Trench. The greater part of the volume of the eastern Atlantic is filled by warmer and less dense waters. These are principally WÜST's (1935) Upper and Middle North Atlantic Deep Water, which take their characteristics from the Mediterranean and the Labrador–Greenland–Scotland area, respectively. Likewise, the Walvis Ridge severely limits the influx of Antarctic Bottom Water to the eastern basin from the south, and the various components of the North Atlantic Deep Water fill the greater part of this basin. The depth of our stratum lies at nearly 5000 m at 20°S.

Southwestern Atlantic

As the surface where $\sigma_4 = 45{\cdot}92$ extends into the South Atlantic and enters the Antarctic Circumpolar Current, its depth decreases (Fig. 6). A geostrophic balance to this current requires strong horizontal density gradients, and all of the isopycnals slope upward to the south. The surface where $\sigma_4 = 45{\cdot}92$ rises from about 3600 m near 20°S to 3000 m near 45°S, not only in the Atlantic but also in the Indian and Pacific oceans. This radial near-symmetry is important to the method we are using: not only does the intersection of the σ_4 - equals - 45·92 surface with the 3000 m level lie in a very narrow zone around Antarctica, but the characteristics of the water along the intersection have a narrow range, and this means that the shift from our σ_4 surface to a σ_2 surface is reasonably well defined. The total range of salinity along this intersection is from 34·72 to 34·82‰ and the corresponding values of σ_2 are from 37·09 to 37·11; a value of σ_2 equal to 37·10 has been chosen to define the stratum farther south, to depths of 1000 m.

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*On a surface defined by a single density parameter the potential temperature is uniquely defined by the salinity, but we have used three density parameters (Fig. 6). A salinity of 34·70‰ on the surface where σ_0 equals 27·83 defines a θ of 0·95°C; where σ_4 equals 45·92, it defines a θ of 1·18°C. Therefore, charts of both S and θ are presented (Figs. 7 and 8), though the features are not very different. We have not resolved all of the minor differences in contouring that may occur in the interpolation of such related fields.

Indian and Pacific oceans

Warm saline water extends eastward from the southwestern Atlantic into the Indian Ocean; north of about 50°S the depth of the stratum is greater than 2 km and it falls rapidly to 3200–3400 m near 30°S (Fig. 6). In the far north the depth is near 4 km. Salinity and temperature decrease northward from about 40°S (Figs. 7 and 8), reflecting the influence of the underlying Antarctic Bottom Water (Fig. 3b). The distribution of temperature and salinity suggests the existence of a western boundary current on the eastern side of Madagascar.

The tongue of warm saline water extends into the Pacific at slightly lower values (cf. GORDON, 1967). There is also a suggestion of a western boundary current near 180° longitude as far as 20°S (WARREN, 1970). Northward from there the stratum lies between the Intermediate Water and the remnant of the Antarctic Bottom Water (Fig. 3c), and the temperature and salinity decrease.

In the North Pacific it is confined to the central area and its depth is greater than 4000 m; vertical gradients are weaker there than elsewhere and its depth is not precisely defined by the data. Below 4000 m the potential temperature is almost constant within the measurement limitations and salinity increases only slightly. Minor errors in salinity measurements can account for vertical displacements of several hundred meters. Indeed, the values of σ_4 below 4000 m in the North Pacific vary but little from the 45·92 that defines this surface; in the North Pacific this stratum represents, in effect, the bottom water.

Around Antarctica

The effect of the warm saline water from the North Atlantic can be seen clearly in the northern Indian and Pacific oceans, but there is substantial evidence of Antarctic characteristics along the southern edge of the warm saline tongue.

The depth of the stratum continues to rise toward the south: the intersection with the 1000 m level lies near 60°S except south of Africa, where it is at about 50°S and in the southeastern Pacific, where it is nearer Antarctica, at about 70°S. Along this intersection, the salinity varies from 34·70‰ to 34·75‰ (Figs. 6 and 7). These S and corresponding θ values are very much like those at 3000 m, and the range of σ_0 they define is from 27·82 to 27·84; a value of 27·83 has been chosen to extend the stratum farther upward and southward. (The lowest values of salinity and temperature along the 1000 m intersection of the σ_2 - equals - 37·10 surface occur in the Scotia Sea. They are about 34·704‰ and 1·11°C, and correspond to a σ_0 value of 27·82. In this region we might have chosen slightly lower values of S and θ, where σ_0 is 27·82, but we believe the differences are not significant.)

In the South Atlantic the lower North Atlantic Deep Water meets the Antarctic Circumpolar Water (SVERDRUP, JOHNSON and FLEMING, 1942), which is a mixture of the Lower North Atlantic Deep Water and water from the colder, less saline Antarctic, principally from the Weddell Sea. This Circumpolar Water extends along the Circum-

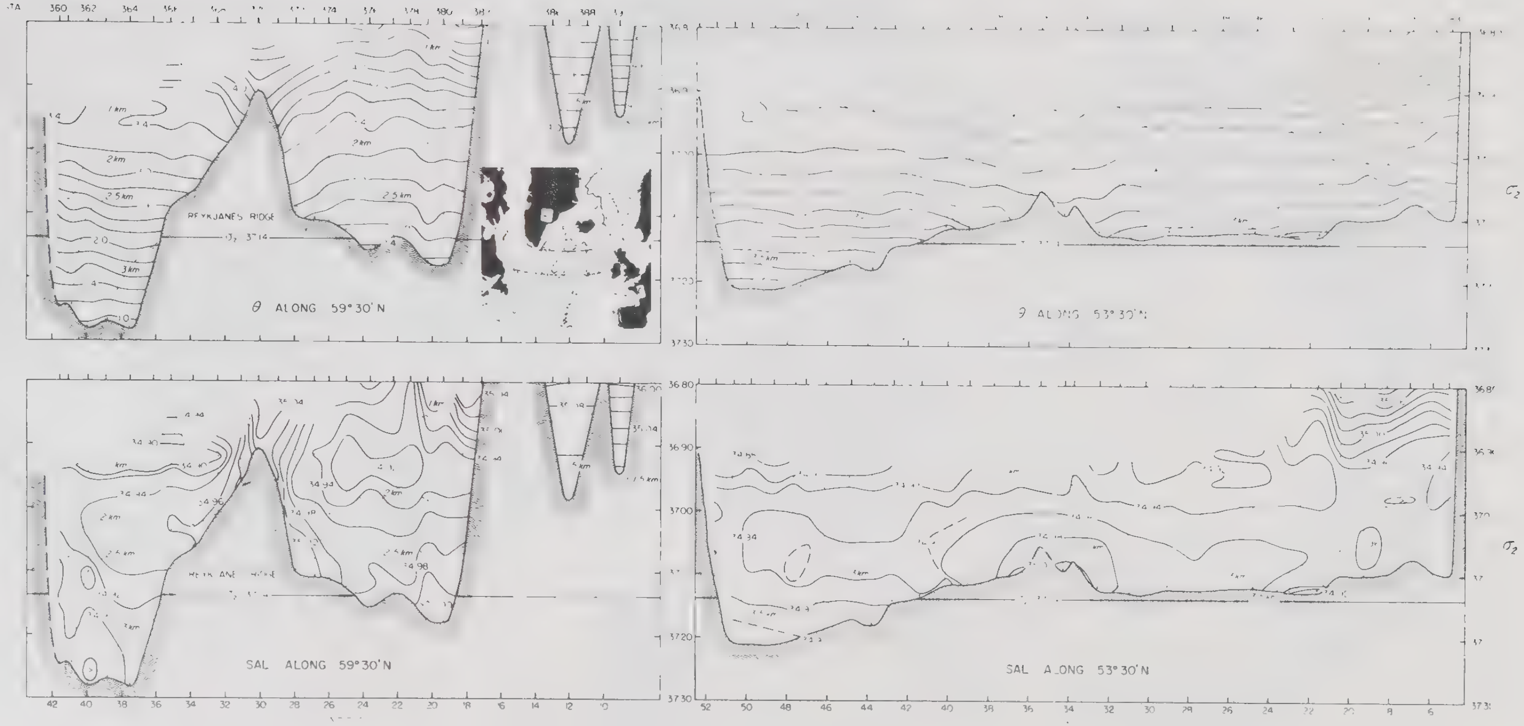

Fig. 5. Vertical sections along 59 30 N and 53 30 N of θ, S, and depth: the ordinate is σ_2. Values at depths greater than 1000 m only are shown

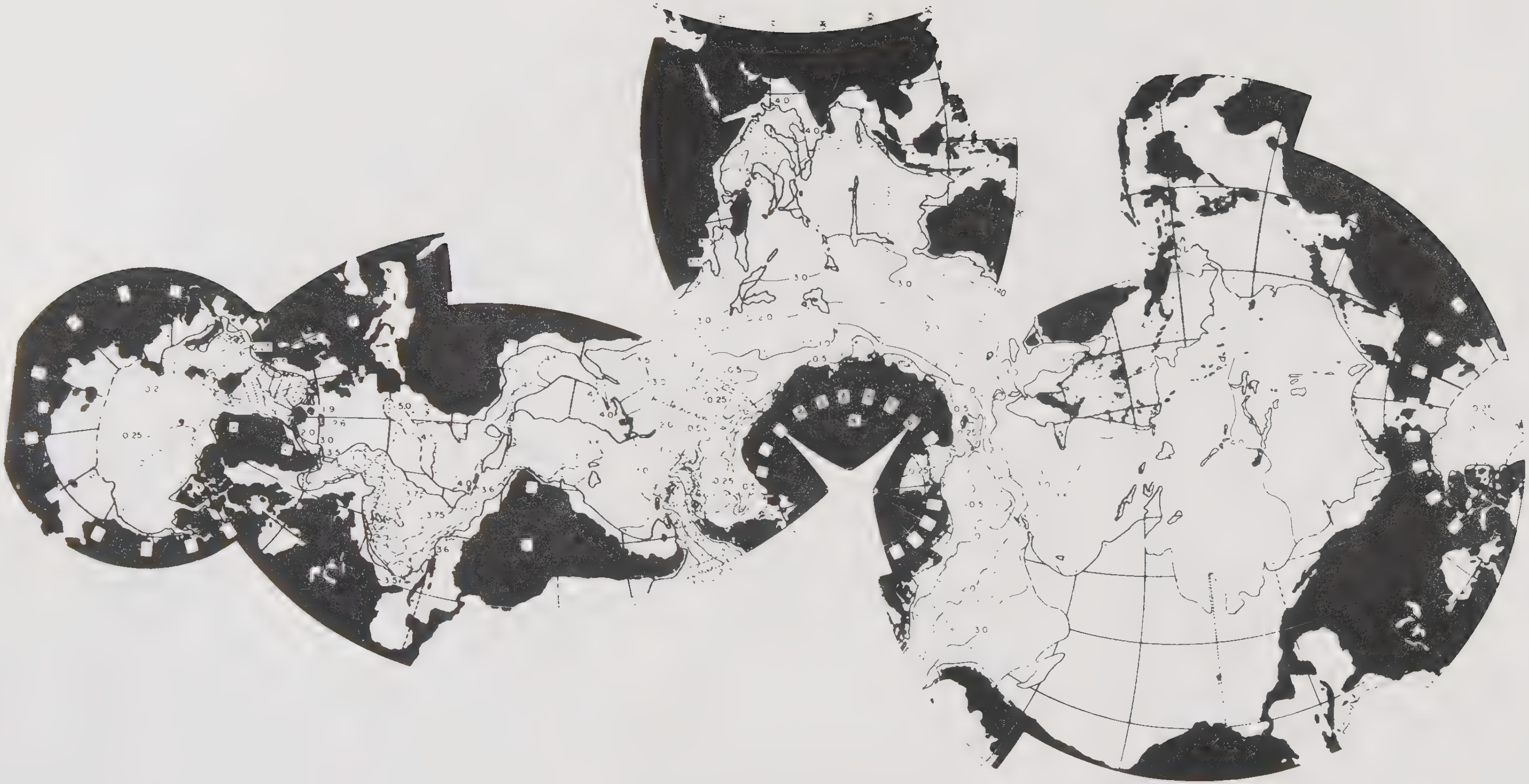
4.0
3.0
0.5
0.25
5.0
3.75
3.6
1.9
2.6
0.2
0.25

Fig. 6 Depth (in km) of the stratum where [illegible] equals 45·92 (below 3 km) and the corresponding [illegible] and values above 3 km. Data are identified in the Appendix.

[1076c]

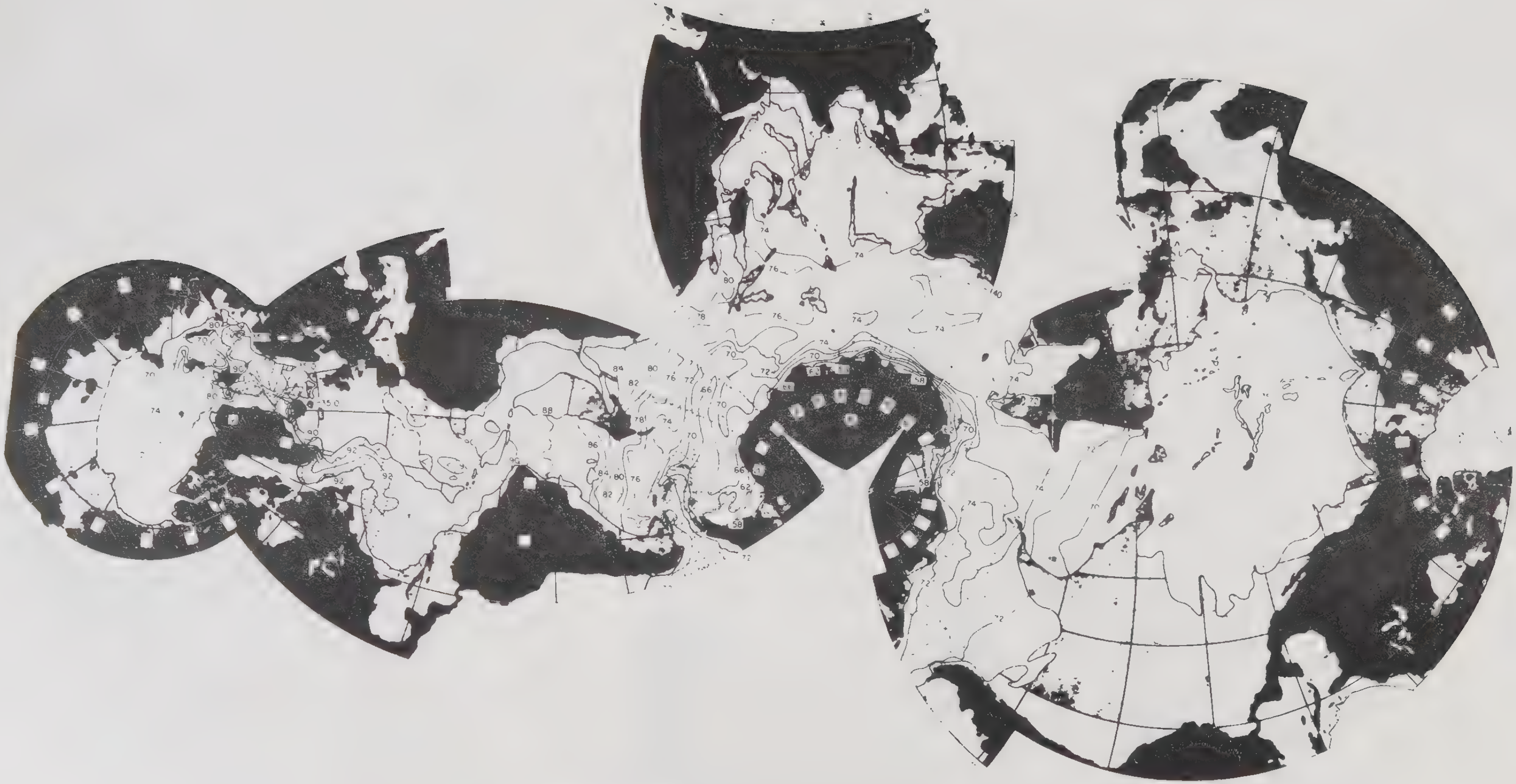

Fig. 7. Salinity (per mille) along the stratum where σ_4 equals 45.92 (below 3 km) and the corresponding σ_2 and σ_3 values above 3 km.

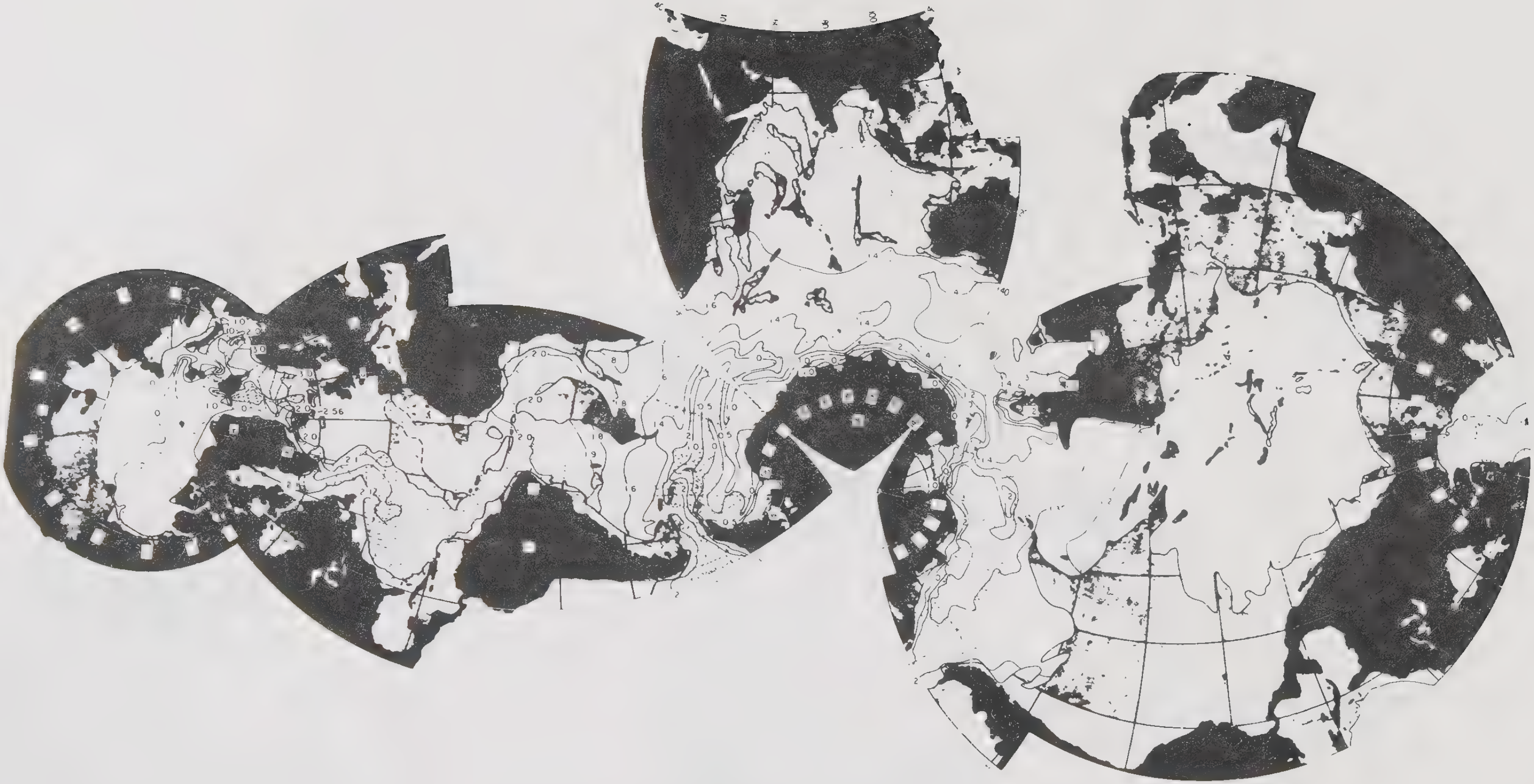

Fig. 8 Potential temperature (°C) along the stratum where [illegible] equals 45.92 (below 3 km) and the corresponding [illegible] and [illegible] values above 3 km

polar Current through the Indian and Pacific oceans as a tongue of water warmer and more saline than the waters on either side (Figs. 7 and 8). It returns to the Atlantic through the Drake Passage (Clowes, 1933; Gordon, 1971). It is this returning water, with S and θ near 34·72‰ and 1·2°C, rather than the colder, fresher waters of the Weddell Sea, that the Lower North Atlantic Deep Water first encounters at the northern limb of the Weddell Sea cyclonic gyre.

The stratum has colder, lower-salinity values where it lies near the surface around Antarctica. In some areas near the coast these values approach the freezing point (about −1·90°C at 34·55‰). However, it is remarkable that the low values do not extend to still lower latitudes, but are interrupted by the high-salinity, warm tongue that extends eastward from the South Atlantic all around Antarctica.

Indeed, a tongue of warm saline water returns westward from the Indian Ocean into the Weddell Sea; the area of less than 250 m along about 60–65°S from 15°E to 50°W longitude appears to be the axis of the Weddell Sea cyclonic gyre, with the shoaling related to the geostrophic circulation. Temperature and salinity are correspondingly low along this axis as a consequence of vertical mixing with the overlying water. However, no salinity less than 34·59‰ or θ less than −0·90°C has been observed on the stratum in that area. The overlying surface salinity there is quite low (mostly less than 34·10‰) and the temperature minimum lies above the 27·83 surface. A general winter overturn to this depth in the gyre seems unlikely.

The stratum intersects the sea surface in a small area near the ice shelf in the southwestern Weddell Sea; at several stations nearby it lies at depths less than 150 m underlying surface water of relatively high salinity (about 34·50‰). It seems likely that in this region (where bottom depth is 500–800 m) a substantial area may have no water with σ_0 as low as 27·83 in winter.

This stratum is shallow north of the Ross Sea in what appears to be a feature comparable to the Weddell Sea gyre. Otherwise, near Antarctica it is slightly shallower than 500 m, except in the Southeast Pacific, where it lies between 500 and 1000 m.

THE PATH OF THE WATERS THAT FILL THE ABYSSAL INDIAN AND PACIFIC OCEANS

The extension of the Lower North Atlantic Deep Water toward the North Pacific is illustrated on a vertical section (Fig. 9) which follows the lateral salinity maximum (Fig. 7) from the North Atlantic through the southern Indian Ocean to the South Pacific and then extends northward with the western boundary current along the Tonga–Kermadec Ridge, and then northward through the North Pacific. The section (Fig. 9) is meant to indicate the source, path, and modification of the more saline waters that fill the abyssal Indian and Pacific oceans. Since the stratum varies in depth but is nearly everywhere deeper than 3 km along this section, the ordinate chosen is σ_4. Since our stratum acquires its extreme characteristics only after two water masses from the Norwegian–Greenland Sea have mixed south of the Denmark Strait, there is not a unique path to follow north of the Strait. The path north of *Erika Dan* Sta. 316 (numbered at the top of the figure near the left) is taken from Fig. 3a, and in the Norwegian–Greenland Sea passes through the area which contains no water of density as low as that of the parameter we use.

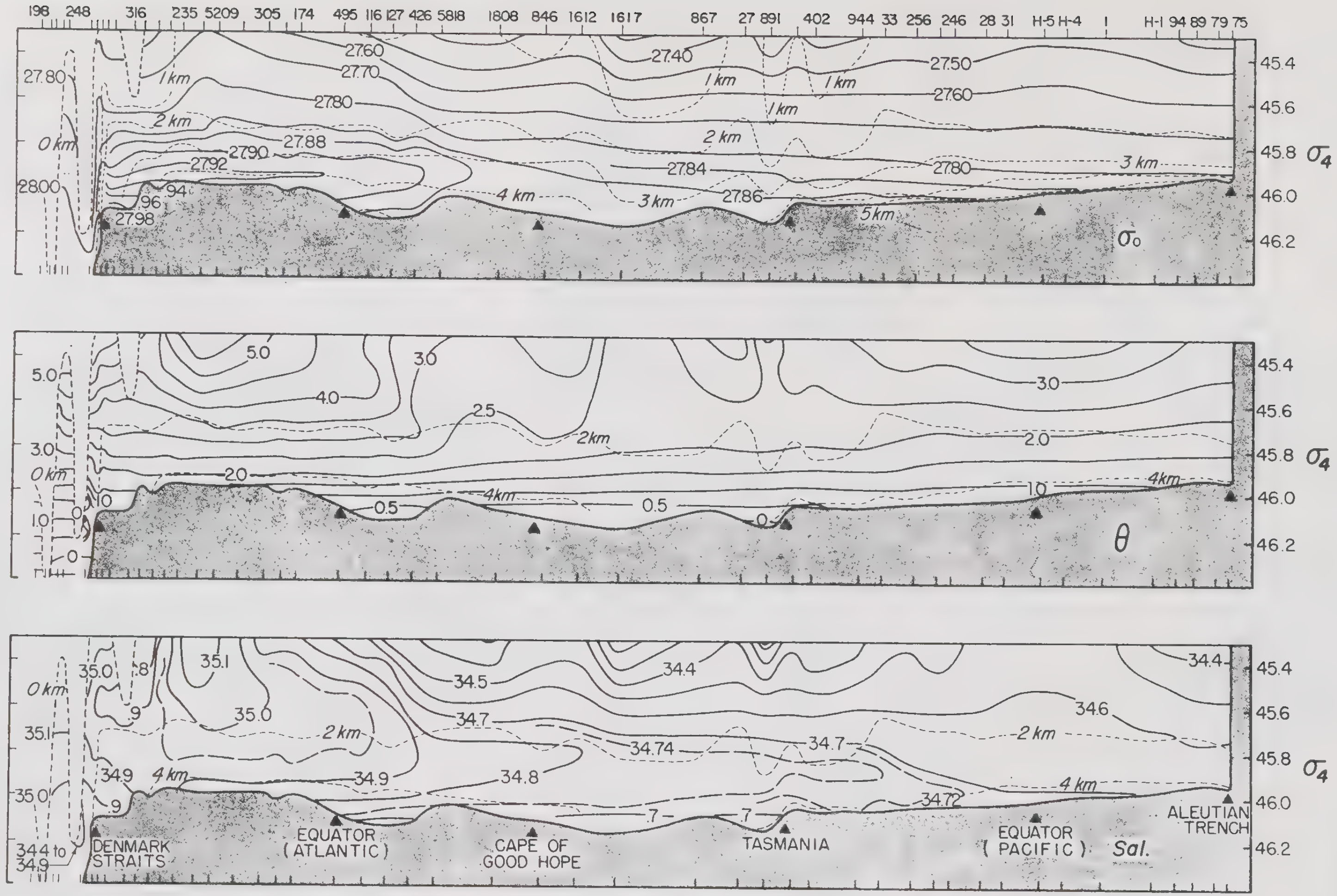

Fig. 9. Potential density, potential temperature, and salinity along a vertical section from the Norwegian Sea to the North Pacific (position of scetion shown in Fig. 2). The ordinate is σ_4, the *in situ* density a parcel of water would have if moved adiabatically to a pressure of 4000 decibars. Depth is shown by the short dashed lines.

Potential density

It is clear that the high potential density near the bottom south of the Denmark Strait has originated in the Norwegian–Greenland Sea. This maximum in σ_0 is seen to be above the bottom (Fig. 9) from about 45°N to the central South Atlantic. As a conservative quantity σ_0 can directly trace the effect of the Norwegian–Greenland Sea water at least this far.

Beyond the Atlantic Ocean σ_0 increases monotonically with depth. There is no comparable source of warm (2°C), saline (34·9‰) water at great depths to maintain this inversion, and vertical mixing along the path results in a general decrease of σ_0 not only at the bottom, but also along the stratum.

Potential temperature

The warmest water of $\sigma_4 = 45{\cdot}92$ is found just south of the Denmark Strait as a consequence of the vertical mixing discussed in a previous section. Everywhere along the path the potential temperature is decreasing with depth at the depth of the stratum. The coldest bottom waters encountered (< 0°C) are at the southernmost segment of the path, south of Australia; from there the path turns abruptly northward, and the bottom temperatures rise monotonically to about 1·1°C in the North Pacific. The potential temperature decreases monotonically along the stratum from the North Atlantic to the North Pacific; this decrease reflects the influence of mixing with the underlying colder bottom water of Antarctic origin.

Salinity

In the Atlantic Ocean the surface where σ_4 equals 45·92 is seen to lie between the great salinity maximum and the less saline bottom waters. Only the deeper, cooler waters of the salinity maximum extend beyond the Atlantic Ocean where the stratum lies close to, but just below, the maximum. North of the Tokelau Trough (near 10°S in the Pacific) the maximum salinity is found at the bottom, and the σ_4 of the bottom water is very nearly 45·92.

DISCUSSION

Lateral effects

There exist two areas where water of the chosen density parameters can be formed at or near the sea surface. One is the Norwegian–Greenland Sea, whose products are vertically mixed at depth southwest of Greenland to form the saline and warm extremes of the stratum. The other area (cold and of low salinity) includes the Weddell Sea and regions along the Antarctic Continent where the stratum lies near the sea surface. The direct effect of the Weddell Sea is seen in the Weddell Sea gyre and its extension into the Indian Ocean. At its extreme the Antarctic influence appears to extend to 30°S in the Atlantic where the lateral gradients steepen. The characteristics of the relatively warm saline waters found in the west central South Atlantic (34·86‰ and 1·9°C) decrease to 34·75‰ and 1·5°C in the mid-Indian Ocean. South of 60°S in the Weddell Sea gyre there is a return flow of moderately warm and saline Circumpolar Water from the Indian Ocean. Elsewhere around Antarctica the strongest lateral gradients are quite close to the continent, indicating that the lateral admixture of the extreme Antarctic water is apparently very limited. In the Indian and Pacific oceans the Circumpolar Current is dominated by the saline, warm water derived from the North Atlantic. The zone of this water extends eastward between 40°S and 60°S in the Indian Ocean and 50°S to 70°S in the Pacific.

It is not clear why the lateral Antarctic influence is so small along this stratum and the North Atlantic influence so great. It has long been recognized that the North Atlantic provides warm, saline water of a particular density range that is found over most of the ocean between the two major products of the Antarctic—the Bottom Water, which is cold and of moderate salinity, and the Intermediate Water, which is of low salinity. This does not mean, of course, that the Weddell Sea does not produce water of the North Atlantic density range, but that the bulk of the water in that range has the characteristics of the North Atlantic rather than of the Antarctic. This warm saline water from the North Atlantic extends laterally upward through the Antarctic Circumpolar Current (where the isopycnals rise abruptly to the south) and mixes with near-surface Weddell Sea water of lower salinity. FOFONOFF (1956) has suggested that the characteristics are such that the mixtures may yield only surface water, shelf water, or Bottom Water, all of different density from the North Atlantic Deep Water: in this sense the Weddell Sea may serve as a sink for some of the saline North Atlantic Deep Water and, in particular, may reduce the mass of water in this density range.

Vertical mixing

In the northern Indian and Pacific oceans the temperature and salinity on this stratum decrease to lower values than in the Circumpolar Water. Since there is no lateral source for this cooling and freshening (no water of this density is formed or found near the sea surface in either area), it must be a result of vertical mixing.

The nature of this vertical mixing, and its relation to lateral flow, can be examined through the differences in the θ–S curves. Vertical mixing is required in all of the northern oceans to account for the characteristics, but it is not immediately obvious that water flowing between an overlying high-salinity layer and an underlying low-salinity layer should become more saline in one area and less saline in another.

The explanation for the sense of change lies in the curvature of the θ–S curve at the stratum. Just south of the Denmark Strait $(\delta^2 S)/(\delta\theta^2)$ is positive; i.e. the curve is concave toward higher salinities (Fig. 10, curve A), and vertical mixing should tend to increase salinity near our density value (and hence potential temperature). Southward from the maximum values on the stratum (about 40°N to 60°N; Figs. 7 and 8) the curvature changes sense: the bottom water is much colder and less saline (as the Antarctic source is approached) and the overlying tremendous salinity maximum decreases through mixing with the Subantarctic Intermediate Water. The water along the stratum meets no lateral source of colder, lower-salinity water and does not change so markedly, hence the change in sense of curvature (Fig. 10, Curve B) that occurs just north of the equator in the Atlantic. The remainder of the figure illustrates the further changes in the θ–S curves along the path. The curves remain concave toward lower salinities, as both the underlying and overlying waters become less saline, until ultimately a nearly straight line is achieved near the equator in the Pacific. At this point, and northward in the Pacific, the water is a nearly linear mixture of the overlying Intermediate Water and the modified remnant of Antarctic Bottom Water. The

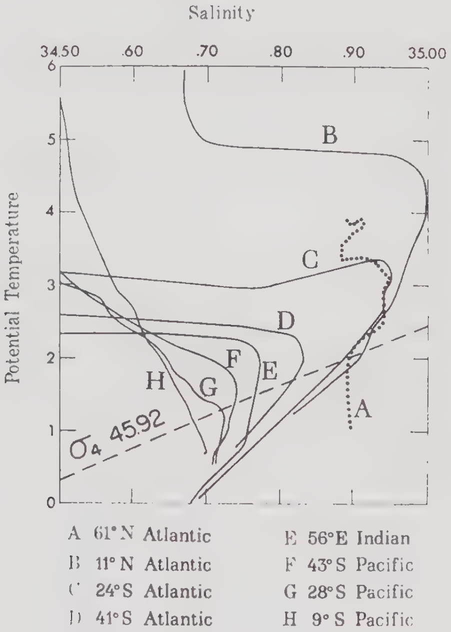

Fig. 10. Temperature–salinity (θ–S) curves at positions along the path of the section shown in Fig. 9.

curvature is gone. This does not mean necessarily that the water in the stratum from the North Atlantic does not extend this far, but that mixing has finally altered its characteristics, and those of the waters above and below, to the extent that a linear θ–S relation exists among the three. Further vertical mixing in the North Pacific cannot destroy the linear relation in the deeper water: its two effects in the northern regions are to mix away the deep end of the line until the final bottom values of about 1·06°C and 34·698‰ are attained, and to swing the upper end of the line toward lower salinities.

Upward flux

If water from the Norwegian–Greenland and Weddell seas sinks from the surface and fills the abyssal Indian and Pacific oceans, then water must rise somewhere, and somewhere there must be vertical flow across the stratum we have defined. It does not seem likely that much upward transport can take place through the salinity tongue. At successively greater distances from the source, the maximum value of salinity is found at higher densities, hence the major erosion of the salinity maximum is by mixing with the overlying lower-salinity water; the deeper values are not so markedly changed.

Where substantial vertical flux takes place, the salinity maximum cannot be maintained. In the northern Indian and Pacific oceans the maximum has disappeared, and these seem to be the most likely places for steady-state upward flux to be important. In the Indian Ocean north of 10°S a source of more saline water lies above the stratum,

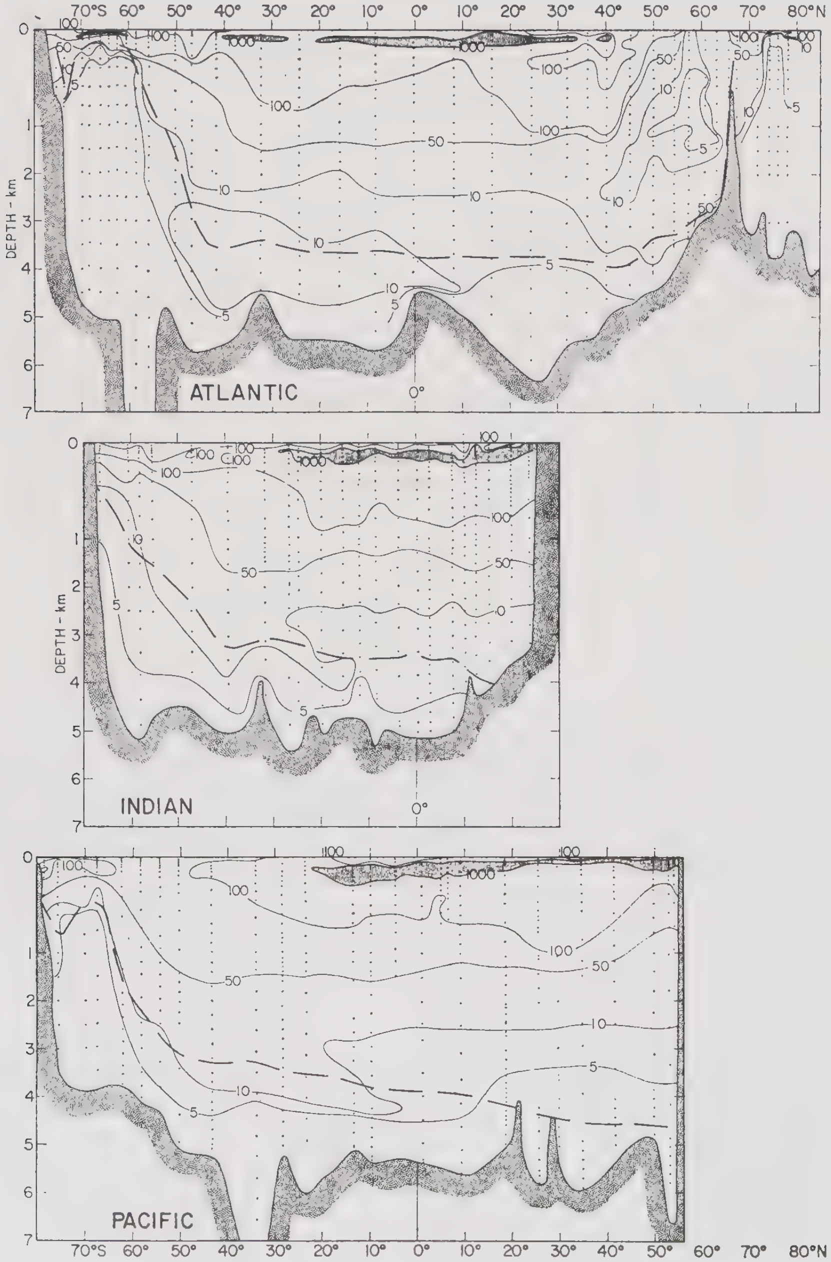

Fig. 11. Stability along the three north–south lines in the Atlantic, Pacific, and Indian oceans. The quantity is $E = \Delta'\rho/\Delta Z$ (10^{-8} g/cm^3/m), after Hesselberg and Sverdrup (1914). The scale of the figure does not allow the details of the upper few hundred meters to be represented; some values near zero occur in the mixed layer and some values much greater than 1000×10^{-8} occur within the pycnocline maximum.

and an upward flux of water is required to balance the downward flux of salt. In the North Pacific Ocean the highest salinity is at the bottom, and an upward flux of more saline water is required to balance the excess precipitation at the surface; these areas have already been shown to require vertical mixing to account for the changes in characteristics on the stratum. Additional vertical mixing with the low-salinity Intermediate Water, with a lateral flow of the mixture southward toward or across the equator, may bring this water to shallower levels and start the return path.

Stability at the depth of the stratum

Upward flow and mixing might be expected to take place most effectively in those areas where they are least opposed by the hydrostatic stability. The quantity examined (Fig. 11) is (after HESSELBERG and SVERDRUP, 1914)

$$E = \frac{\Delta'\rho}{\Delta Z}$$

where the $\Delta'\rho$ (g/cm^3) indicates the density difference that would exist between a pair of vertically adjacent samples if the deeper sample were moved adiabatically to the level of the upper sample (a distance of ΔZ, in meters). If one assumes an accuracy of about 10^{-5} g/cm^3 for the calculations of density, an error in E of about 10^{-5} g/cm$^3/\Delta Z$ must be expected. In the deeper parts of the ocean the vertical spacing of samples is typically 300–500 m; the error in E is thus about 2 or 3×10^{-8} g/cm^3/m in typical data observed at this interval. (If the stability were calculated from two parcels 2 km apart vertically, the resolution would be improved and would show the Antarctic to be much more stable than the Norwegian–Greenland Sea, as the stratification in S and θ (Fig. 3a) would suggest.) The values within the 5×10^{-8} contour have no coherent pattern, but merely represent measurement error about some low value of E. From Fig. 11 it appears that the thickest layers of low-stability water are found in the Antarctic, the Norwegian–Greenland Sea, and the North Atlantic between 40° and 60°N and above 3000 m. The first two are recognized as areas where relatively low-density water from near the surface is made colder and more saline, resulting in the formation of dense bottom water; the net vertical transport of water in those areas is downward. In the third, substantial stirring and vertical flow may occur, but the layer does not extend deep enough to remove the bottom water.

The Atlantic section is not significantly different from SCHUBERT'S (1935) section, except that it includes the Norwegian–Greenland Sea and more Weddell Sea daat, The stratum we are investigating is in a fairly stable part of the column as it extends southward from the Denmark Strait; its deep-water maximum in stability is at 60°N at 3000 m depth, where the Norwegian–Greenland Sea water has cascaded over the ridge beneath the less dense waters.

The remaining layers of low stability are found in the deeper parts of the North Indian and the North Pacific oceans. Of these the North Indian is slightly more stable. possibly because of its limited latitudinal extent and the higher temperature in the upper 2000 m. In the Pacific north of 20°N, the very weak vertical temperature gradient (in spite of the opposing salinity gradient) provides the thickest layer of low stability ($< 5 \times 10^{-8}$) surrounding our stratum.

The sudden decrease in stability at about 10°S in the Pacific, through the North

Tokelau Trough (REID, 1969), might be considered a consequence of a blocking of the deepest, densest water. Some possible effect of this is seen (Fig. 3c), but the saline water in the bottom of the North Pacific ($> 34{\cdot}70‰$) shows that the water has been influenced by the North Atlantic; its low temperature ($< 1{\cdot}0°C$ in potential temperature) shows a clear effect of the Antarctic Bottom Water. Thus, both North Atlantic Deep Water and Antarctic Bottom Water must enter this region of low stability in the North Pacific. Whether the Trough actually precludes the movement of the densest part of this mixture or merely enforces further vertical mixing to weaken the vertical gradients has not yet been examined. Higher densities are observed in the South Pacific ($\sigma_4 > 46{\cdot}10$; Fig. 3c) than appear in the eastward-flowing water in the Drake Passage (REID and NOWLIN, 1971), indicating that the densest water entering the South Pacific south of Australia must be subject to vertical mixing and must depart, either northward or eastward, at a reduced density.

CONCLUSION

Water originating in a zone of high potential density forms a lateral extension of σ_0 (a conservative quantity) as a maximum above the bottom. Vertical mixing of the waters above and below cannot create or maintain such a feature, but can only dissipate it. The feature extends laterally for (at least) 10,000 km along the western Atlantic before the mixing has sufficiently smoothed θ and S to eliminate the σ_0 maximum. A salinity maximum in the vertical distribution is found in the Atlantic, and it clearly extends, below the surface, with no other source of high salinity, from the North Atlantic to the equatorial Pacific. Vertical mixing or flow can only dissipate this maximum: its maintenance against vertical dissipation is by lateral processes, which maintain the maximum over a distance of 36,000 km.

Although the stratum occurs in the water column all the way from the North Atlantic to the North Indian and North Pacific, it does not necessarily follow that we are dealing with the same water for the entire distance. The bottom water becomes less dense as it extends northward in all oceans (except the North Atlantic north of 30° to 40°, where a new source is met) (LYNN and REID, 1968). This is accomplished by vertical mixing of the bottom waters with those above them. Actually a net vertical flow is required upward from the bottom water to account for the continuous input of bottom water from the Weddell and Norwegian–Greenland seas. Water must somewhere be moving upward across our stratum, and, since the density distribution appears to be steady, a downward diffusion of the characteristics leading to lower density is required.

It can be argued that what we have done by extending this density parameter to the North Indian and North Pacific oceans is to intercept the mixture of North Atlantic Deep Water with Antarctic Bottom Water at the point where its density, decreasing with time, has just achieved the value we have chosen. We believe, however, that the long extensions of the potential-density maximum and the salinity maximum, and the related change in curvature of the θ–S diagrams, may be taken to imply that this interception of new water is limited to the northern parts of the Indian and Pacific oceans. To the extent that this is true, this exercise is useful in examining the deeper circulation.

While vertical processes ultimately limit the concentrations, the very broad-scale lateral extensions of various water masses lead us to believe that lateral processes play a very significant role; vertical processes alone could not create such features nor do they immediately eliminate them. Lateral processes cannot create all of the characteristics of such features, nor dissipate those which terminate at the ocean bottom. What we seem to see is local formation through either vertical or lateral processes, extension over wide areas by lateral movement and mixing, and ultimate dissipation by both lateral and vertical mixing and flow. There is some reason to believe that the northern Indian and (particularly) the northern Pacific are regions where vertical dissipation is most important.

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APPENDIX

We have used about 3700 hydrographic stations out of more than twice that many we considered. Our choices favored observations using salinometers, observations from large expeditions, and winter data (in high latitudes), though it was necessary to use many data not fitting these criteria.

The data were obtained through the U.S. National Oceanographic Data Center. The stations used are too numerous to list in detail, but the great majority are identified below. (Numbers in parentheses are N.O.D.C.'s index numbers.)

Arctic Ocean: Almost all data available through N.O.D.C. archives to 1969 that reached the depth of the stratum.

Norwegian and Greenland seas: Anton Dohrn 1957, 1958, 1959 (060001, 9, 918); *Erika Dan* 1962 (310170); *Gauss* 1958 (580005, 13); *Helland-Hansen* 1958 (58908, 41); *Johan Hjort* 1958 (580035, 957).

Atlantic Ocean north of 40°S*:* All of the I.G.Y. expeditions used in Fuglister (1960); Gulf Stream '60 (Fuglister, 1963) (310974), *Meteor* (060004); and from the Equalant expeditions the *Crawford* (310993), *Explorer* (310990), *Geronimo* (310995) and *Pillsbury* (310996).

Indian Ocean north of 40°S*: Africana* (91050); *Anton Bruun* (31918); *Argo* (310181, 184, 269); *Atlantis* (31197), *Diamantina* (09001, 2, 3, 4, 7, 29); *Discovery* (74007, 30, 37, 40); *Meteor* (06007); *Natal* (91040, 44), *Pioneer* (31201); *Serrano* (31090); *Vema* (31834); *Vityaz* (90010, 32, 34).

Pacific Ocean north of 40°S*: Alexander Agassiz* (311219); *Argo* (311181, 2); *Atlantis* (311219); *Brown Bear* (310558); *Dana* (26009); *Discovery* (740702); *Eltanin* (311212); *Gascoyne* (09005, 33); *George B. Kelez* (310852): *Horizon* (310802); Norpac (310346); *Pioneer* (310099, 945); *Rehoboth* (310685); *Ryofu Maru* (491219); *Spencer F. Baird* (311217); *Vityaz* (900589, 861, 862); and as yet unpublished Scripps Institution data from Nova, Styx, Spheres, and Kiki expeditions.

Southern Ocean south of 40°S*: Argo* (31181); Deep Freeze II (31561, 90), III (31593), '61 (31672), '62 (31867, 951); *Deutschland* (06044); *Discovery* (74037, 38, 39, 40, 702); *Eltanin* (311212); *Glacier* (318057); *Meteor* (06004); *Norvegia* (58006); *Vityaz* (90004, 830); and unpublished Scripps Institution data from the Piquero expedition.

Because the data are from various times, methods, and institutions, it has been necessary to do some smoothing in order to achieve the contours seen on the maps. In the Norwegian and Greenland seas, where the stratum lies at shallow depths and time variations may occur, we have selected mostly winter and spring data from 1957–59. Beneath the Gulf Stream the data show more fine-scale variation than the figure can illustrate, though the variations are of marginal significance. In the tropical Indian Ocean the data showed a broader range than we have mapped, but no coherent patterns were suggested and we believe that the broad range stems from diversity of method and quality, and that the values shown are not misleading, though the shapes of the contours may be. Between 40°S and 60°S in the eastern Indian Ocean two areas of low θ and S ($< 1{\cdot}4$°C, $< 34{\cdot}74$‰) are shown in the midst of the saline, warm tongue (Figs. 7 and 8). This is the best resolution we could make of the available data; it is likely to be altered as newer data appear.

Additional and connecting stations to complete the World Ocean section.

Ship	*Originator's Sta. #*	*Lat.*	*Long.*	*NODC Id. #*
Atlantis	5462	11°27′N	50°34′W	310751
Crawford	426	24°20′S	29°38′W	310831
Atlantis	5818	32°35′S	26°45′W	310837
Discovery	1808	41°36′S	0°29′E	740040
	846	40°41′S	23°02′E	740038
	1612	40°28′S	39°03′E	740040
	867	49°26′S	98°22′E	740038
Diamantina	27	44°04′S	122°34′E	090007
Discovery	891	56°03′S	135°11′E	740038
Eltanin	682	51°51′S	150°23′E	318035
	402	54°00′S	159°54′E	310790
Discovery	944	47°42′S	178°16′W	740038

Station list for vertical sections.

Ship	*Originator's Sta. #*	*Lat.*	*NODC Id. #*
	Atlantic Ocean		
G. O. Sars	198	78°16′N	580013
	185	76°18′N	
	179	74°30′N	
	318	72°00′N	580050
Johan Hjort	248	70°45′N	580957*
Anton Dohrn	1595	67°33′N	060001
	2268	65°50′N	060918
	2283	65°15′N	*
	2313	62°19′N	
	2317	61°00′N	
Erika Dan	316	57°26′N	310170
	320	54°26′N	
	339	49°27′N	
Discovery	3520	45°17′N	740622
Crawford	235	40°15′N	310623
Chain	44	36°17′N	310207
Atlantis	5209	32°01′N	310566
Discovery	3615	24°31′N	740622
Crawford	305	16°14′N	310623
	174	8°14′N	310583
	495	0°15′S	310831
	116	8°18′S	310583
	127	15°45′S	
	423	24°16′S	310831
Atlantis	5812	32°26′S	310837
Discovery	72	41°43′S	740035
Eltanin	170	46°50′S	310707
	176	50°21′S	
	131	55°54′S	
	145	58°34′S	
Discovery	1994	60°36′S	740040
	1996	62°32′S	
	1998	64°16′S	
	2000	66°00′S	
	2002	68°19′S	
	2004	69°50′S	
Deutschland	64	73°34′S	060044
	61	75°22′S	
	Indian Ocean		
Anton Bruun	191	23°57′N	310372
Discovery	5067	20°13′N	740007
Atlantis	64	15°18′N	310197
Discovery	5387	12°42′N	740030
Argo	62	10°14′N	310269
	57	7°39′N	310269
	31	2°59′N	310184
	Indian Ocean (cont.)		
Atlantis	139	0°13′N	310197
	144	3°43′S	
	165	8°30′S	
Argo	86	12°00′S	310269
Atlantis	205	15°28′S	310197
	735	20°01′S	310247
	741	24°56′S	
Argo	109	26°51′S	310184
Atlantis	767	31°59′S	310247
	766	32°00′S	
Argo	111	39°45′S	310184
Discovery	1617	47°22′S	740040
	1622	55°37′S	
	2113	58°23′S	
	857	60°40′S	740038
Thorshavn	6	66°34′S	580812
	Pacific Ocean		
Brown Bear	52	54°03′N	310748
Pioneer	75	53°11′N	310099
	79	49°51′N	
	89	41°32′N	
	94	34°46′N	
Argo	H–1	29°36′N	(Zetes)
	H–3	25°44′N	(Nova)
Horizon	1	18°45′N	(Spheres)
Argo	H–4	9°17′N	(Nova)
H. M. Smith	33	8°03′N	310465
	30	5°06′N	
Argo	H–5	1°05′N	(Nova)
Stranger	25	4°00′S	310724
A. Agassiz	31	9°33′S	(*Styx*)
	28	13°25′S	
Gascoyne	246	23°25′S	090033
Eltanin	145	28°19′S	311212
Gascoyne	256	33°52′S	090033
Eltanin	33	43°12′S	311212
	327	50°01′S	310707
	329	54°00′S	
	337	58°03′S	
	341	62°01′S	
Discovery	2232	67°10′S	740040
	1267	69°49′S	740039
Staten Is.	8	75°25′S	310672
Discovery	1644	78°25′S	740040

*Only bottom values were used.

7143

HARMONIC FUNCTIONS FOR SEA-SURFACE TEMPERATURES AND SALINITIES, KOKO HEAD, OAHU, 1956-69, AND SEA-SURFACE TEMPERATURES, CHRISTMAS ISLAND, 1954-69

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ABSTRACT

Harmonic functions have been fitted to time-series, sea-surface temperatures and salinities in order to facilitate studies of the oceanographic climate near Hawaii and Christmas Island. The manner in which Fourier analysis has been adapted to this application has been described. The standard errors of estimate for Koko Head temperatures and salinities are less than 0.26° C and less than 0.05‰, respectively. The standard errors of estimate for Christmas Island temperatures are approximately 60 % above those for the Koko Head temperature. The expected values of the Koko Head temperature and salinity functions have an uncertainty of ±0.1° C and ±0.015‰, respectively, when samples are obtained twice weekly. Error terms of the Christmas Island temperatures, with daily sampling, are on average 0.07° C. Harmonic analysis spanning the entire sampling duration shows that long-term variations in the Christmas Island temperature and Koko Head salinity are larger than the seasonal variations. Seasonal variations in the Koko Head temperatures are dominant and longer term variations small. The results of the harmonic analyses are presented in the appendixes: (1) a listing of coefficients that define the Koko Head temperature and salinity functions for each year and the Christmas Island temperature functions for each quarter of each year, (2) graphs of the fitted curves together with the observed values for each year.

In this paper harmonic functions are presented of sea-surface temperatures and salinities that have been regularly measured near Koko Head, Oahu (lat. 21°16′ N., long. 157°41′ W.) since 1956 and at Christmas Island (lat. 1°51′ N., long. 157°23′ W.) since 1954 (Fig. 1).

Sea-surface temperatures and salinities change in response to, and therefore reflect, sea-air interaction processes (heat exchange, evaporation minus precipitation) and oceanographic processes (advection, diffusion). For example, the mean sea-surface temperature for a month at Koko Head provides a measure of the mean heat content of the water near the surface. Thus, if the mean temperature for March is above that for February, then meteorological and oceanographic processes must have taken place to raise the mean heat content of

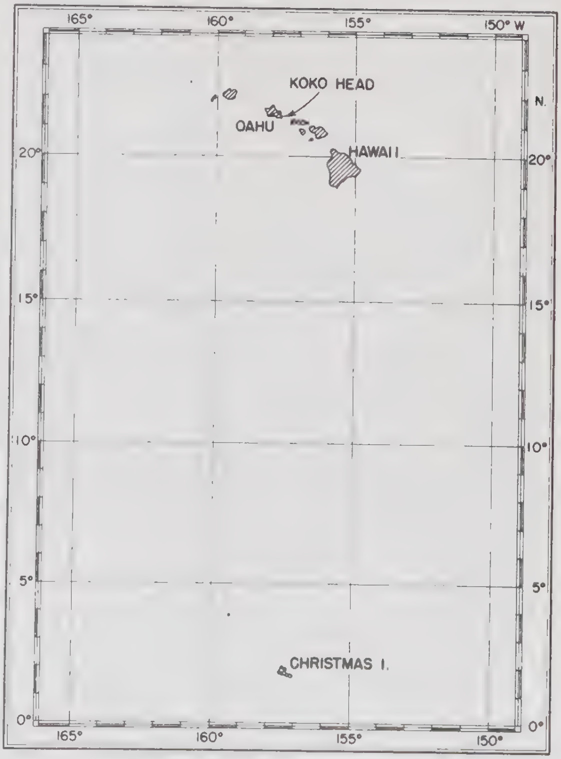

Figure 1.—Location of Koko Head, Oahu and Christmas Island.

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the surface water in March above that in February. This concept was used in studies of the Hawaiian oceanographic climate (Seckel, 1962, 1969) and has been applied to Hawaiian fishery problems (Seckel and Waldron, 1960; Seckel, 1963).

Rigorously, the theory of distribution of properties in the sea states that the change of sea-surface temperature during a time interval, say from the first day of one month to the first day of the next month, is equal to the integral of all meteorological and oceanographic processes affecting the temperature during the time interval:

$$\theta_b - \theta_a = \int_a^b (\text{all processes})\, dt.$$

θ_a is the temperature at the beginning and θ_b is the temperature at the end of the interval. In application, the choice of θ_a and θ_b presents the following problems: The difference in the observed temperatures at times a and b also reflects the effect of short-term variability ("noise") that is not of interest in monitoring the large-scale events. If one uses monthly mean temperatures in the heat budget equation that include observations made 15 days before and after times a and b, then the change of temperature incorporates the effect of processes that lie outside the interval of interest. Although mean values usually provide an adequate measure of the temperature change during given time intervals, the true change of temperature can be obscured. One can overcome the problems caused by the two unsatisfactory methods of obtaining measures of the temperature change by finding suitable functions that filter out undesirable short-term variability without obscuring the basic temperature and salinity trends.

Techniques that can be used in the smoothing of time series data have been reviewed by Holloway (1958) and usually involve moving averages of the data to which weighting factors have been assigned.

Curve fitting provides another method of approach. A useful technique that has been used in this report, is to obtain an analytic expression for the temperature and salinity as a function of time by Fourier analysis. The Fourier series is efficiently, and therefore inexpensively, derived by computer. Efficiency is furthered in that graphs can be produced by automatic plotter. The Fourier series provides a least-squares fit of the observed values. It permits filtering of undesired variability, facilitates statistical evaluation of the data, and—within limits—provides insight into the properties of the distribution.

These advantages will become apparent in the following sections of this report. The results of the analyses for each year of observation are presented in the appendix in both tabular and graphical form.

THE FOURIER METHOD

Fourier series are well known, widely applied, and adequately described in texts of advanced calculus. A good description can be found in Sokolnikoff (1939) where the derivation of the Fourier coefficients by least-squares method is also presented.

The temperature or salinity is expressed as a function of time, t, in the Fourier series:

$$S_n(t) = \frac{A_0}{2} + \sum_n (A_n \cos n\omega t + B_n \sin n\omega t), \quad n = 1,2,3, \ldots k$$

where $\omega = \dfrac{2\pi}{T}$, and T is the fundamental period. For example, if harmonic analysis is to be performed on data collected for a duration of 1 year, T would be 365 days.

The Fourier series contains the coefficients A_0, A_n, and B_n that are given by the Fourier integrals

$$A_n = \frac{2}{T} \int_0^{t=T} F(t)\cos(n\omega t)dt, \quad n = 0,1,2, \ldots k,$$

and

$$B_n = \frac{2}{T} \int_0^{t=T} F(t)\sin(n\omega t)dt, \quad n = 1,2,3, \ldots k.$$

The coefficient A_0 is the special case of A_n with $n = 0$. In our application $F(t)$ is the temperature or salinity at the time t. Of course, the functional relationship between temperature and time or salinity and time is not known so that

$F(t)$ is the observed temperature or salinity at the time t. Furthermore, $F(t)$ is known only at finite intervals of time so that the above Fourier integrals must be obtained by numerical integration. This integration, approximating the area under the curves $F(t)$ cos $(n\omega t)$ and $F(t)$ sin $(n\omega t)$, is performed by summing areas of rectangles with height $G(t)$ cos $(n\omega t)$ or $G(t)$ sin $(n\omega t)$, and with width Δt, the sampling interval.

The finite difference form of the Fourier integrals is

$$A_n = \frac{2}{T} \sum_{i=1}^{m} G(t)_i \cos(n\omega t)\Delta t_i, \quad n = 0,1,2, \ldots k,$$

and

$$B_n = \frac{2}{T} \sum_{i=1}^{m} G(t)_i \sin(n\omega t)\Delta t_i, \quad n = 1,2,3, \ldots k.$$

The number of samples in the interval $t = 0$ to $t = T$ is $m + 1$,

$$\Delta t_i = t_i - t_{i-1},$$

and $G(t)_i = \frac{1}{2}[F(t_i) + F(t_{i-1})], \quad i = 1,2,3, \ldots m.$

The time used to evaluate the geometric factor is $\frac{1}{2}$ $(t_i + t_{i-1})$. Other schemes of obtaining the best estimate of $G(t)$ cos $(n\omega t)$ during the interval Δt can be used but would not significantly affect the results in our application (see Kaplan, 1953: p. 168-172).

Library programs for the evaluation of Fourier coefficients by computer usually require that the sampling interval, Δt, be constant. Since this condition is not necessarily met in our application, a more flexible computer program was written to evaluate the coefficients. In this program the sampling interval may vary, and the number of samples for the basic period of analysis need not be the same in each application.

The Fourier coefficients evaluated in the above manner enable us to describe analytically the temperature or salinity as a function of time. If we wish to go further and gain insight into the properties of the temperature or salinity distribution, it is more useful to express the Fourier series as a sum of cosines:

$$S_n(t) = \frac{A_0}{2} + \sum_n C_n \cos \omega(nt - \alpha_n), \quad n = 1,2,3, \ldots k.$$

The transformation is accomplished by the use of the trigonometric indentities

$$A_n = C_n \cos \omega\alpha_n,$$

$$B_n = C_n \sin \omega\alpha_n,$$

$$C_n = \pm(A_n^2 + B_n^2)^{1/2},$$

and $$\omega\alpha_n = \arctan \frac{B_n}{A_n}.$$

In the application described in this report the fundamental period in the Fourier series is the sampling duration or any portion of this duration that may be arbitrarily chosen; the amplitudes and phase angles do not necessarily coincide with natural variations in temperature or salinity; and the harmonic functions have no predictive value.

In some cases, such as the Koko Head temperatures with a well-defined annual cycle, the fundamental period of the Fourier series derived for each year approximates the annual cycle. At Christmas Island, however, an annual temperature cycle is not always clearly apparent. Despite the fact that choice of the fundamental period may be arbitrary and may not coincide with a naturally occurring period, the spectrum is resolved beyond the first few harmonics. For example, if the fundamental period, $n = 1$, is 12 months then the period of the first harmonic, $n = 2$, is 6 months. A naturally occurring 9 months cycle in the observations would in this case not be resolved. As n increases, however, resolution improves to 4, 3, 2.4, 2, etc., months.

The highest harmonic, or n-value, to which harmonic analysis can be carried, is limited by the number of observations. In the ideal case and when samples are equally spaced in time, there must be at least $2n$ observations, i.e., at least two samples per cycle. In nature, where we are dealing with noncyclical variations and unequal spacing of samples a sinusoidal curve cannot be resolved with only two samples, and a minimum of four or, better, six samples is required to achieve good resolution. For example, sea-surface temperatures are to be monitored and the fundamental period of observations is to be 12 months. Resolution of a 1-month cycle ($n = 12$), requires four samples per month, or sampling once per week.

APPLICATION OF THE FOURIER METHOD

In practice, the Fourier method described above must be adapted to each specific application. In addition to the minimum number of samples necessary in order to attain a desired resolution another restriction applies to variations in the sampling interval. Although the computer program used to obtain the results of this paper allows a varying sampling interval, thus accepting a sequence with missing observations, the sampling interval can be allowed to vary only within limits. For example, at least four samples per month are necessary to resolve a monthly cycle. This cycle will, however, not be resolved if the samples are taken on four consecutive days, rather than being evenly distributed throughout the month. It is also possible to aid the harmonic analysis in rapid convergence to its best fit with the observed values by adjusting the fundamental period of analysis and by performing some preliminary operations which are described below.

APPLICATION TO KOKO HEAD SEA-SURFACE TEMPERATURES AND SALINITIES

The sampling station is located near Koko Head at the exposed, eastern shore of Oahu so that the sea-surface temperatures and salinities measured there reflect open-ocean conditions. The salinities appear to be affected by runoff only on rare occasions of heavy rainfall. Both the temperatures and salinities are based on bucket samples. The salinity is determined in the Hawaii Area Fishery Research Center, Honolulu.

Before 1961 samples were collected at weekly intervals and subsequently twice weekly, usually on Tuesday and Friday mornings. Occasionally sampling has been missed. The computer program must therefore accept data with an irregular sampling interval.

The basic period for analysis has been chosen to be 1 year. Harmonic analysis began with the first sample and ended with the last sample of the year. The sampling time, in days and months, was converted to days of the year beginning with the first of the year.

Owing to a longer term trend, the value of a property at the beginning is not necessarily the same as at the end of an annual cycle. In the case of Koko Head salinities and Christmas Island temperatures, it will be seen later that an annual cycle is, in fact, not always apparent. The noncyclic trend during the analysis period can be obtained by linear approximation. Rapid convergence to the best fitting function can then be achieved by performing the harmonic analysis on the residuals of the observed values from a linear fit.

In our application the first observed value, $F(t_0)$, and the last observed value, $F(t_l)$, for the period were used to obtain the linear equation

$$S' = F(t_0) + bt$$

where $$b = \frac{F(t_l) - F(t_0)}{t_l - t_0} .$$

The residuals, $R_m = F(t_m) - [F(t_0) + bt_m]$, $m = 0.1,2, \ldots l$, were used to obtain the Fourier coefficients. The Koko Head temperatures and salinities for each year are then expressed by the function

$$S = K + bt + \sum_{n=1}^{k} C_n \cos\omega(nt - \alpha_n)$$

where $$K = F(t_0) + \frac{A_0}{2} \text{ and } \omega = \frac{2\pi}{T} .$$

The phase angles and coefficients for each of the years 1956-69 of the sea-surface temperatures are listed in appendix A Table 1, and of the sea-surface salinity are listed in appendix A Table 2.

The functions for each year together with the observed values of the sea-surface temperature and salinity have been drawn by automatic plotter and are presented in appendix B.

Quality control of the data was achieved by two passes of the data through the computer. First, the fitted graphs and plots of the observed values as well as listed deviations of observed values from the functions that resulted from the first computer analysis were used to reject obviously erroneous observations. The analysis was then repeated without the rejected observations. The tabulations in appendix A and figures in appendix B are the result of the second pass through the computer. The rejected values are plotted and identified in the figures of appendix B.

APPLICATION TO CHRISTMAS ISLAND SEA-SURFACE TEMPERATURES

The Christmas Island sea-surface temperatures are measured with a bucket thermometer each morning (about 0900 local time) in the channel leading from the open sea to the lagoon. The differences between open sea and lagoon water temperatures have not been determined. It is reasonable to assume that these temperatures differ, and so introduce variability in the observed temperature as tidal currents in the channel change from day to day. The tide-induced variability will, however, not be reflected by a harmonic function where the resolution of the highest harmonic is longer than 1 month. Although the sampling site is not ideal, the observed temperatures are believed to reflect, with some bias induced by lagoon temperatures, the changes of sea-water temperature from month to month.

The procedure to obtain functions of the Christmas Island temperatures was the same as that used for the Koko Head temperatures and salinities with the exception that a different fundamental period was chosen. In contrast to Koko Head where an annual cycle dominates the sea-surface temperature, longer term changes dominate the temperature at Christmas Island. The basic temperature pattern at Christmas Island also changes from year to year. For these reasons a duration of 120 days was chosen as fundamental period and Fourier analysis was performed, as before, on the residuals of the observed values from a linear fit.

For each year, the 120-day periods followed in sequence with an overlap of 30 days. The periods ran from the first day of the year to day 120, from day 91 to day 210, from day 181 to day 300, and from day 271 to day 390, extending 25 days into the following year. In this manner rapid convergence of the harmonic function to the best fit was obtained.

With daily sampling and a fundamental period of 120 days, harmonic analysis could be carried to the harmonic $n = 30$, but to do so would introduce variability that we wish to smooth out. Although a resolution of 1 month requires harmonic analysis to $n = 4$ only, the analysis was arbitrarily carried out to $n = 7$, resolving a period of 16 days.

The resulting phase angles and coefficients for 1954-69 of the sea-surface temperature are listed in appendix C. The functions for each year together with the observed values have been drawn by automatic plotter and are presented in appendix D.

Quality control procedures were identical to those for the Koko Head analyses. Relatively large data gaps occurred at Christmas Island in 1964, 1967, and 1968. Because some observations were available during each of the 120-day periods in question, harmonic analysis produced coefficients that enabled drawing of curves in appendix D although there were no data. These curves were not erased since it is instructive to see what harmonic analysis will do when faced with insufficient data.

DISCUSSION OF RESULTS

In this paper we are concerned with the derivation and presentation of harmonic functions of regularly observed sea-surface temperatures and salinities at fixed stations rather than with oceanographic interpretations. In the discussion of the results we will, therefore, concern ourselves primarily with the quality of fit of the functions. We will also briefly discuss some properties of the temperature and salinity distributions that are reflected by the functions and, finally, show functions spanning the entire time of observations.

QUALITY OF FIT

A superficial inspection of the figures in appendixes B and D shows that the harmonic functions follow the trend of the observed values very well. Closer inspection, however, reveals that there are cases where the fitted curves depart from the observed trend. An example occurred when the Koko Head salinity function (appendix B) for 1956 fluctuated about the observed values from day 145 to day 180. The fluctuations were caused by a data gap between these days. A 15-day data gap is too large when harmonic analysis resolves a period of 1 month. Another example of deviations occurred in the Christmas Island temperature function (appendix D) for 1968 between day 240 and day 275. Again, a 30-day data gap is too large when harmonic analysis resolves a period of 19 days.

These examples illustrate that the sampling interval in harmonic analysis may vary only within limits and that the interval of permissible sampling gaps depends upon the period resolved by the analysis. In cases such as were cited, where the fundamental period of analysis is much longer than the sampling gap, it is possible to constrain the harmonic function by inserting "dummy" values based on linear interpolation of the last sample before, and the first sample after, the data gap.

There are cases where the fitted curve fails to follow the observed trend. When the deviations from the fitted curves are relatively large, there is a tendency to reject the observed values during quality control procedures, blaming the deviations on erroneous sampling. Temperature deviations of this type occurred at Koko Head during days 65 to 90 of 1967. First the observed temperatures fell to 0.6° C below the fitted curve and then rose abruptly 1.3° to 0.6° C above the fitted curve. Erroneous sampling is ruled out since more than one sample was involved in establishing the trend that was abruptly broken and, in addition, the salinity showed similar variability during the same time interval. First the observed salinity rose to 0.15‰ above the expected value and then dropped abruptly 0.37‰ to 0.16‰ below the expected value. In the Hawaiian region the temperature increases and the salinity decreases southward. Thus, northward-southward displacements of the water that would result in the observed temperature and salinity changes were the probable cause for the large deviations rather than sampling error.

In order to assess the quality of fit quantitatively, we will consider several aspects of the standard error of estimate (root mean square deviations of the observed from the expected values). This statistical parameter is listed in three tables for each function, with harmonic analysis carried out for the fundamental period, the first harmonic, the second harmonic, etc. ($n = 1,2,3, \ldots$). Table 1 applies to Koko Head temperatures, Table 2 to Koko Head salinities, and Table 3 to Christmas Island temperatures.

In each case the listed standard error of estimate decreases or reaches a constant value with increasing n. The fit of the function therefore improves or levels off as the analysis is carried out to higher harmonics. Exceptions to this trend occurred in 1956, 1959, and 1961 when the standard errors of estimate for the Koko Head salinity functions (Table 2) increase as the highest n values are reached. Prior to May 1961, only four or five samples per month were obtained at Koko Head and therefore the highest n value permitted by the sampling frequency had been reached. In addition, sampling gaps occurred in 1956, as mentioned before, and in 1961 between days 220 and 241.

The fit of the Koko Head temperature functions (Table 1) improves most rapidly during the first few harmonics and with analysis carried out to $n = 6$, the standard error of estimate is near or below 0.3° C. With analysis carried out to $n = 13$, the standard error of estimate is below 0.2° C for all years excepting 1963 and 1965-68.

Greatest improvement of fit for the Koko Head salinity functions (Table 2) does not always occur during the first few harmonics but continues as analysis is carried beyond $n = 6$. In 1960, for example, the standard error of estimate with analysis to $n = 1$, $n = 6$, and $n = 13$, is 0.090‰, 0.075‰, and 0.038‰, respectively. The standard error of estimate at the n value of best fit in Table 2 is below 0.04‰ except

TABLE 1.—Standard error of estimate (° C) for each annual temperature function at Koko Head, 1956-68, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1956	0.21	0.19	0.17	0.16	0.16	0.14	0.14	0.14	0.13	0.13	0.12	0.12	0.11
1957	0.36	0.29	0.24	0.24	0.23	0.23	0.23	0.21	0.20	0.20	0.19	0.19	0.18
1958	0.31	0.29	0.24	0.24	0.22	0.22	0.22	0.22	0.22	0.20	0.20	0.18	0.17
1959	0.41	0.38	0.29	0.29	0.26	0.24	0.24	0.24	0.22	0.21	0.20	0.20	0.19
1960	0.30	0.27	0.24	0.24	0.23	0.23	0.22	0.22	0.19	0.19	0.17	0.16	0.15
1961	0.47	0.37	0.35	0.33	0.32	0.31	0.31	0.28	0.24	0.23	0.20	0.18	0.17
1962	0.32	0.25	0.25	0.25	0.23	0.21	0.21	0.21	0.20	0.19	0.19	0.19	0.17
1963	0.30	0.29	0.28	0.28	0.27	0.26	0.23	0.23	0.21	0.21	0.21	0.21	0.21
1964	0.29	0.29	0.28	0.25	0.25	0.24	0.23	0.21	0.20	0.18	0.17	0.17	0.16
1965	0.49	0.45	0.38	0.36	0.34	0.30	0.28	0.27	0.27	0.27	0.27	0.26	0.26
1966	0.43	0.32	0.32	0.30	0.30	0.27	0.27	0.27	0.26	0.26	0.26	0.26	0.26
1967	0.44	0.40	0.34	0.33	0.32	0.27	0.26	0.25	0.25	0.24	0.24	0.24	0.23
1968	0.37	0.32	0.28	0.28	0.28	0.27	0.26	0.25	0.24	0.24	0.23	0.23	0.23

TABLE 2.—Standard error of estimate (‰) for each annual salinity function at Koko Head, 1956-68, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1956	0.045	0.034	0.032	0.031	0.031	0.030	0.030	0.029	0.028	0.025	0.025	0.028	0.030
1957	0.068	0.057	0.054	0.054	0.045	0.041	0.039	0.037	0.034	0.034	0.032	0.030	0.030
1958	0.069	0.066	0.059	0.059	0.056	0.053	0.053	0.052	0.049	0.048	0.041	0.036	0.036
1959	0.174	0.099	0.076	0.075	0.074	0.073	0.069	0.064	0.060	0.058	0.054	0.053	0.054
1960	0.090	0.083	0.081	0.078	0.077	0.075	0.069	0.063	0.056	0.053	0.050	0.042	0.038
1961	0.064	0.061	0.051	0.047	0.043	0.038	0.037	0.036	0.033	0.030	0.027	0.028	0.028
1962	0.049	0.046	0.046	0.044	0.043	0.041	0.037	0.037	0.036	0.035	0.034	0.034	0.034
1963	0.054	0.053	0.052	0.046	0.045	0.045	0.043	0.041	0.037	0.037	0.034	0.033	0.033
1964	0.086	0.078	0.069	0.063	0.061	0.059	0.052	0.052	0.051	0.044	0.044	0.043	0.038
1965	0.094	0.085	0.078	0.072	0.072	0.071	0.066	0.064	0.058	0.056	0.054	0.048	0.045
1966	0.044	0.043	0.042	0.037	0.037	0.034	0.034	0.033	0.033	0.030	0.030	0.029	0.028
1967	0.079	0.078	0.074	0.072	0.068	0.061	0.055	0.054	0.052	0.051	0.050	0.046	0.044
1968	0.060	0.052	0.051	0.046	0.042	0.040	0.038	0.038	0.035	0.035	0.033	0.033	0.033

TABLE 3.—Standard error of estimate (° C) for each quarterly temperature function at Christmas Island, 1954-68, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 7.

		N-VALUES						
YEAR	QUARTER	1	2	3	4	5	6	7
1954	1	0.44	0.41	0.41	0.41	0.32	0.30	0.29
	2	0.36	0.35	0.33	0.33	0.32	0.30	0.30
	3	0.51	0.50	0.50	0.50	0.47	0.45	0.44
	4	0.39	0.38	0.37	0.33	0.30	0.30	0.29
1955	1	0.30	0.28	0.27	0.26	0.26	0.26	0.25
	2	0.29	0.29	0.28	0.28	0.28	0.27	0.26
	3	0.34	0.33	0.33	0.33	0.32	0.32	0.32
	4	0.46	0.45	0.43	0.42	0.40	0.39	0.39
1956	1	0.40	0.38	0.38	0.37	0.36	0.35	0.35
	2	0.52	0.50	0.48	0.48	0.46	0.45	0.45
	3	0.48	0.47	0.45	0.44	0.43	0.41	0.41
	4	0.38	0.38	0.36	0.36	0.36	0.32	0.32
1957	1	0.48	0.46	0.45	0.44	0.43	0.43	0.43
	2	0.61	0.54	0.54	0.54	0.53	0.51	0.51
	3	0.44	0.44	0.43	0.43	0.40	0.39	0.38
	4	0.40	0.39	0.35	0.34	0.33	0.30	0.28
1958	1	0.26	0.25	0.24	0.24	0.24	0.23	0.23
	2	0.33	0.33	0.33	0.32	0.31	0.30	0.29
	3	0.37	0.35	0.30	0.29	0.28	0.28	0.28
	4	0.32	0.31	0.28	0.27	0.26	0.25	0.25
1959	1	0.41	0.34	0.30	0.28	0.28	0.27	0.27
	2	0.40	0.38	0.36	0.35	0.34	0.34	0.33
	3	0.48	0.39	0.36	0.34	0.32	0.32	0.32
	4	0.43	0.39	0.36	0.32	0.31	0.29	0.29
1960	1	0.30	0.29	0.27	0.26	0.26	0.25	0.25
	2	0.35	0.33	0.32	0.31	0.31	0.31	0.31
	3	0.32	0.31	0.30	0.27	0.26	0.26	0.25
	4	0.39	0.32	0.29	0.26	0.26	0.24	0.23
1961	1	0.36	0.34	0.34	0.32	0.31	0.30	0.27
	2	0.34	0.34	0.31	0.27	0.26	0.26	0.25
	3	0.36	0.29	0.29	0.28	0.27	0.25	0.25
	4	0.26	0.24	0.22	0.22	0.20	0.19	0.18
1962	1	0.39	0.34	0.30	0.30	0.30	0.27	0.27
	2	0.38	0.33	0.31	0.30	0.29	0.27	0.25
	3	0.26	0.24	0.21	0.20	0.20	0.19	0.19
	4	0.30	0.26	0.25	0.24	0.24	0.24	0.24
1963	1	0.36	0.36	0.34	0.34	0.32	0.32	0.28
	2	0.46	0.38	0.31	0.30	0.28	0.27	0.21
	3	0.36	0.29	0.29	0.27	0.26	0.25	0.24
	4	0.30	0.29	0.28	0.26	0.26	0.25	0.25
1964	1	0.32	0.32	0.31	0.30	0.29	0.29	0.28
	2	0.37	0.31	0.30	0.29	0.28	0.28	0.27
	3	0.34	0.31	0.29	0.29	0.28	0.27	0.26
	4	0.28	0.27	0.26	0.23	0.22	0.21	0.21
1965	1	0.30	0.29	0.28	0.27	0.26	0.25	0.25
	2	0.36	0.32	0.29	0.29	0.29	0.29	0.29
	3	0.53	0.52	0.45	0.42	0.39	0.38	0.37
	4	0.37	0.32	0.31	0.30	0.30	0.30	0.29
1966	1	0.42	0.39	0.35	0.34	0.33	0.30	0.29
	2	0.42	0.35	0.35	0.34	0.34	0.31	0.30
	3	0.60	0.51	0.48	0.46	0.43	0.42	0.40
	4	0.68	0.68	0.53	0.52	0.51	0.51	0.47
1967	1	0.42	0.40	0.34	0.34	0.34	0.32	0.32
	2	0.40	0.39	0.36	0.36	0.36	0.36	0.35
	3	0.39	0.38	0.37	0.36	0.34	0.33	0.33
	4	0.32	0.30	0.28	0.27	0.27	0.27	0.26
1968	1	0.42	0.37	0.36	0.33	0.33	0.33	0.32
	2	0.37	0.35	0.31	0.31	0.31	0.30	0.30
	3	0.2[illegible]	0.29	0.29	0.30	0.31	0.28	0.29
	4	0.28	0.27	0.26	0.24	0.23	0.21	0.21

in 1959 and 1965 when it is 0.054‰, and 0.045‰, respectively.

At Christmas Island (Table 3), the average standard error of estimate at $n = 4$ (resolution of 1 month) is near 0.33° C and therefore about 60 % higher than that for the Koko Head temperatures. As previously mentioned, high temperature variability is to be expected at the Christmas Island sampling site.

A standard error of estimate based on all samples used to obtain a function obscures the month-to-month changes in variability that may have occurred. At Koko Head the month-to-month changes in temperature variability as reflected by the standard error of estimate for each month ranges from 0.05° to 0.45° C, the same values for the Koko Head salinities range from 0.006‰ to 0.136‰, and those for Christmas Island temperatures range from 0.17° to 0.66° C. Assuming that sampling error remains constant, the range of variability reflects changes in oceanographic conditions.

The standard error of estimate computed from the temperature and salinity observations of each month also reflects sampling quality in that low values indicate the residual variability in the ocean plus sampling error. For the Koko Head temperature, low values of the monthly standard error of estimate are near 0.1° C and for the Koko Head salinity they are near 0.02‰. The sampling error is therefore within ±0.1° C for the temperature and ±0.02‰ for the salinity. These are the limits to be expected when bucket sampling of the temperature and salinity is carefully done.

Finally, how is the quality of fit affected by sampling frequency and how reliable are the expected values that may be obtained from the harmonic functions? The constraint imposed by the sampling frequency on the resolution that may be attained by harmonic analysis has already been discussed. The present question concerns improvement of fit when the sampling frequency is increased above the minimum requirements.

At Koko Head the sampling frequency was increased from once to twice weekly in 1961. No significant change can be seen in the standard errors of estimate listed in Tables 1 and 2 as a result of doubling the sampling frequency. This observation is consistent with results obtained from oceanographic data collected at Ocean Weather Station "P" in the Gulf of Alaska. Tabata (1964: Table 8) lists the monthly mean value and the standard deviation of the temperature at 10-m depth based on data obtained twice daily, data obtained every second, third, fourth, fifth, sixth, and seventh day of July 1959 and May 1961. For July 1959 the mean temperatures range from 10.70° to 10.81° C and the standard deviations range from 0.60° to 0.76° C. For May 1961 the mean temperatures range from 5.84° to 5.90° C and the standard deviations range from 0.39° to 0.46° C.

In May 1961 Koko Head temperatures and salinities were sampled on 25 days. The mean of all temperature observations was 24.67° C with standard deviation 0.27° C. The mean of temperatures taken every fifth day was 24.58° C with standard deviation 0.39° C. The mean of all salinity observations was 34.759‰ with standard deviation 0.051‰. The mean of salinities taken every fifth day was 34.772‰ with standard deviation 0.058‰. The temperature results from Koko Head are comparable to those from Ocean Weather Station "P" in that mean values and standard deviations based on different sampling frequencies fall within approximately the same range. The standard errors of estimate for the May 1961 Koko Head temperatures and salinities, based on the harmonic functions with resolution of 1 month, are lower than the standard deviations, namely, 0.25° C and 0.027‰, respectively. The standard errors of estimate as well as the standard deviations do not change significantly when the sampling frequency is increased above the required minimum to attain a desired resolution by harmonic analysis.

Increasing the sampling frequency does, however, improve the confidence limits of a mean value or the expected value of a harmonic function. A good measure of the confidence limits of a mean value is the standard error of the mean (the standard deviation divided by the square root of the number of samples). Returning to Tabata's table the standard error of the mean for July 1959 is for twice daily sampling every day 0.086° C, and for twice daily sampling every seventh day 0.253° C. For the same sampling frequencies in May 1961 the standard errors of the mean are 0.053° and 0.15° C, respectively. For the May 1961 Koko Head temperatures the standard error of the mean is 0.055° C with 25 samples and 0.16° C with sampling every fifth day. The standard error of the mean for the May 1961 Koko Head salinities is 0.010‰ with 25 samples and 0.024‰ with sampling every fifth day. On the basis of these considerations, the expected values obtained from the temperature functions have an uncertainty of ±0.10° C, and those from the salinity functions have an uncertainty of ±0.015‰ when samples are obtained twice weekly.

At Christmas Island temperatures are sampled daily rather than twice weekly as at Koko Head. In consequence, despite the larger variability, expected values obtained from the harmonic functions have approximately the same uncertainty as those obtained from the Koko Head harmonic functions. This statement is confirmed by considering the error terms that can be obtained by taking the difference of the expected values at the midpoint of the 30-day overlap portion of the Christmas Island temperature functions (see appendix D). On average this error term is 0.07° C and ranges from 0 to 0.26° C.

SOME PROPERTIES OF THE TEMPERATURE AND SALINITY DISTRIBUTIONS

Although the harmonic functions are merely analytic expressions of the temperature and salinity as a function of time, they do provide, to some extent, insight into the nature of the distributions. For instance, the monthly standard error of estimate, mentioned in the previous section, provides a measure of the month-to-month changes in variability. At Koko Head there is no seasonal pattern in this variability of the temperature; however, there is a seasonal pattern in the variability of the salinity. The monthly standard errors of estimate of the salinity function with harmonic analysis carried out to $n = 13$, are listed in Table 4.

Table 4.—Standard error of estimate (‰) for each month, 1956-68, of the Koko Head salinity. Harmonic analysis is carried out to $n = 13$.

	MONTH											
YEAR	1	2	3	4	5	6	7	8	9	10	11	12
1956	0.030	0.017	0.027	0.048	0.064	0.052	0.024	0.008	0.012	0.014	0.014	0.015
1957	0.049	0.013	0.021	0.015	0.030	0.034	0.029	0.017	0.036	0.031	0.018	0.034
1958	0.006	0.041	0.052	0.049	0.059	0.026	0.028	0.028	0.013	0.023	0.044	0.022
1959	0.049	0.035	0.044	0.136	0.040	0.036	0.054	0.023	0.047	0.032	0.023	0.035
1960	0.042	0.032	0.018	0.019	0.056	0.043	0.075	0.035	0.033	0.014	0.014	0.024
1961	0.036	0.019	0.017	0.019	0.027	0.054	0.011	0.020	0.025	0.021	0.023	0.023
1962	0.054	0.040	0.064	0.021	0.013	0.023	0.025	0.033	0.031	0.031	0.018	0.027
1963	0.029	0.026	0.018	0.073	0.045	0.036	0.021	0.025	0.020	0.022	0.032	0.036
1964	0.031	0.033	0.031	0.030	0.029	0.019	0.035	0.050	0.053	0.052	0.024	0.036
1965	0.044	0.053	0.059	0.092	0.032	0.043	0.034	0.016	0.018	0.033	0.019	0.019
1966	0.026	0.016	0.011	0.014	0.022	0.021	0.011	0.012	0.016	0.033	0.065	0.036
1967	0.026	0.029	0.097	0.055	0.050	0.015	0.019	0.021	0.017	0.031	0.029	0.056
1968	0.034	0.024	0.057	0.041	0.040	0.019	0.035	0.026	0.018	0.021	0.016	0.038

In each year excepting 1957, 1964, and 1966, highest variability occurred during the first 7 months of the year. In 1957 a seasonal pattern was not clearly apparent and in 1964 and 1966 highest variability occurred during the last 5 months of the year. Although the seasonal pattern of variability has not been examined in detail, it is consistent with the results of previous studies (Seckel, 1962, 1969). First, Hawaii is located in the vicinity of a relatively high salinity gradient that delineates the boundary of the North Pacific Central Water. Thus, the salinity measured at the Koko Head sampling station is sensitive to variations in the location of this water type boundary. Secondly, northward displacement of water (warm advection) tends to occur during the first 7 months of the year. In consequence the water type boundary that generally lies south of the Koko Head sampling station during autumn and winter is brought to within the vicinity of the sampling station. The months with higher variability tend to be associated with declines in the Koko Head salinity.

Insight into the nature of the distributions is also obtained by examining the spectra of the harmonic functions. It is evident from the figures in appendix B, that considerable temperature and salinity variability at Koko Head occurs with timespans of 35 to 60 days. Rather than showing the amplitudes for each harmonic of every function, the 13-year mean of the absolute magnitude of amplitudes for each harmonic of the Koko Head temperature and salinity functions is presented in Figure 2.

For both the temperature and the salinity, the amplitude of the annual cycle ($n = 1$) is largest. The amplitudes then decline rapidly with increasing harmonics to $n = 5$. In the case of the temperature, a slight increase in amplitude occurs at $n = 6$ and $n = 9$. Similar small increases in amplitudes occur in the case of the salinity at $n = 7$ and $n = 9$. The increased amplitudes at $n = 6$ and $n = 7$, resolving 60- and 52-day periods, reflect the climatic signals described by Seckel (1962, 1969). The increased amplitude at $n = 9$, resolving a 41-day period, reflects shorter term variability that may be due to large geostrophic eddies with dimensions near 200 km (Wyrtki, 1967) or eddying flow near the Hawaiian Islands.

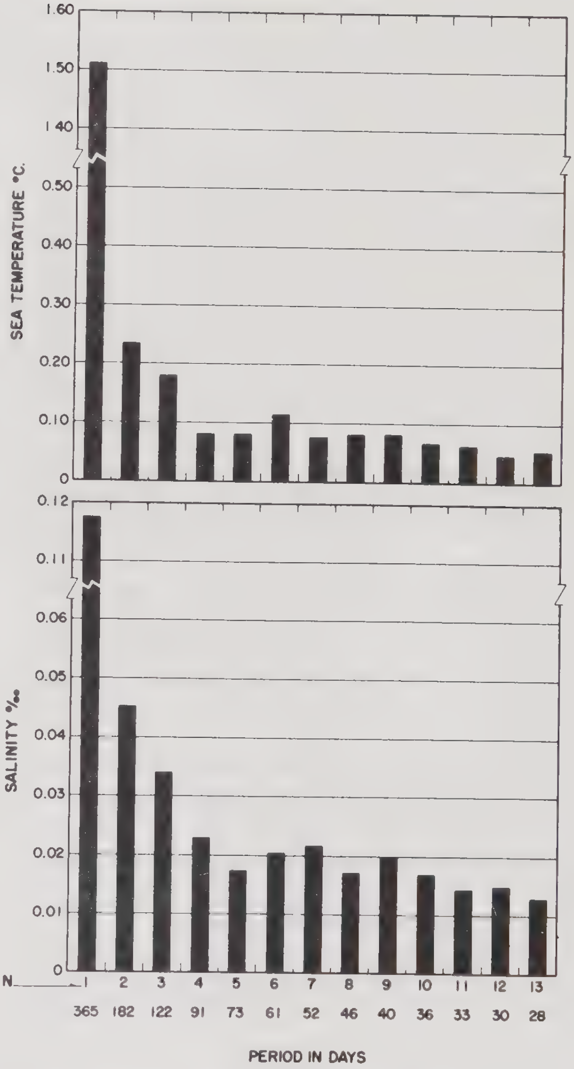

FIGURE 2.—Mean magnitude of amplitudes for each harmonic of the Koko Head temperature and salinity functions, 1956-69.

LONG-TERM HARMONIC FUNCTIONS

Long-term harmonic functions with the fundamental period spanning the entire duration of observations, can be obtained by the method described before in this paper. Temperatures and salinities were used as computed for the

1st and 16th of each month from the harmonic functions whose phase angles and coefficients are tabulated in appendixes A and C. Harmonic analysis was carried to $n = 42$ for the Koko Head temperature and salinity, and $n = 48$ for the Christmas Island temperature, giving in each case a 4 months' resolution. The fitted curves resulting from this analysis are shown in Figure 3, together with the values that were used as input data. Clearly the annual cycle forms the dominant signal in the Koko Head temperature curve. In the Koko Head salinity and Christmas Island temperature curves longer term changes are more pronounced than the annual cycle.

The relatively large deviations of the input data from the long-term function are to be expected. The figures of appendixes B and D show that variations with a duration of less than 4 months can be relatively large and are not resolved by the long-term analyses made.

The spectra of the long-term harmonic functions for the Koko Head temperatures and salinities and the Christmas Island temperatures are shown in Figure 4.

As is also apparent from Figure 3, the spectrum of the Koko Head temperature function is distinct from those of the Koko Head salinity and Christmas Island temperature functions. In the former the 12-month period has the most pronounced amplitude, but in the latter two, although the annual period has a large amplitude, the amplitudes of longer period changes are large and for some periods exceed those of the annual period.

CONCLUSION

The results of this paper show that sea-surface temperatures and salinities regularly monitored at island sampling stations can be expressed by harmonic functions of time. Advantages of analytic expressions for the temperature and salinity were cited in the introduction. Important applications will be in climatic oceanography where one may wish to filter out undesired "background noise." At Christmas Island, for example, the short-term variability with a duration of 1 month or less can be filtered out by using only the harmonic terms to $n = 3$ in the quarterly functions. At Koko Head, the variability with duration of less than 50 days, that may be due to large geostrophic or island-induced eddies, can be filtered out by using only the harmonic terms to $n = 7$ in the annual functions.

We mentioned in the introduction that the rates of change of temperature reflect the climatic processes of change and that distortions or aliasing may occur when monthly mean temperatures are used to compute the change of a property. Consider, for example, the Christmas Island temperatures from March to May 1968 (appendix D, days 61 to 152). In Table 5 are listed the monthly mean observed temperatures, the month-to-month changes of mean temperature, the expected temperatures from the harmonic functions for the 16th of each month (computed with harmonic terms up to $n = 4$), and the month-to-month changes of expected temperatures. It is clear from this illustration that the use of mean values would result in an underestimate of the rise in temperature from March to April, and would obscure the decline in temperature from April to May. The example is not isolated and other instances can be found in both the Koko Head and the Christmas Island data.

TABLE 5.—Month-to-month temperature differences using mean observed temperatures and expected temperatures from the harmonic function, Christmas Island, March to May 1968.

Date	Mean temperature	Change of mean temperature	Expected temperature	Change of expected temperature
	° C	° C	° C	° C
March 1968	25.1		25.1	
		0.9		1.2
April 1968	26.0		26.3	
		0.2		−0.3
May 1968	26.2		26.0	

The results also aid in the choice of an optimum sampling frequency. Both the desired confidence limit and the desired resolution must be considered. If the harmonic functions are to be used in monitoring the oceanographic climate as is the case of those presented in this paper, then the limits of about ±0.1° C for the expected temperature value and ±0.02‰ for the expected salinity value are adequate. As-

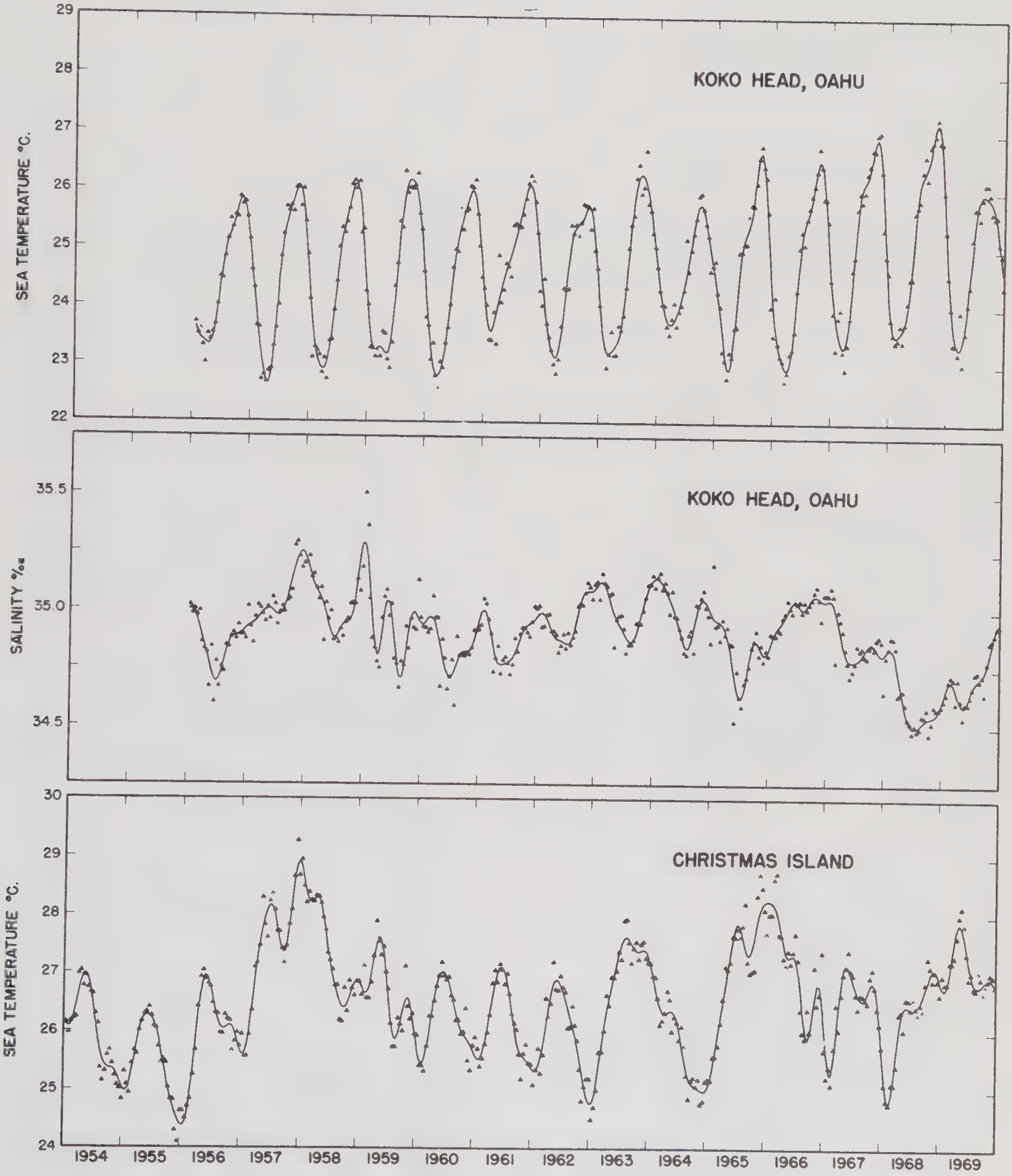

FIGURE 3.—Fitted curves with 4 months' resolution of the Koko Head temperature, 1956-69, Koko Head salinity, 1956-69, and the Christmas Island temperatures, 1954-69. Input data are indicated by small triangles.

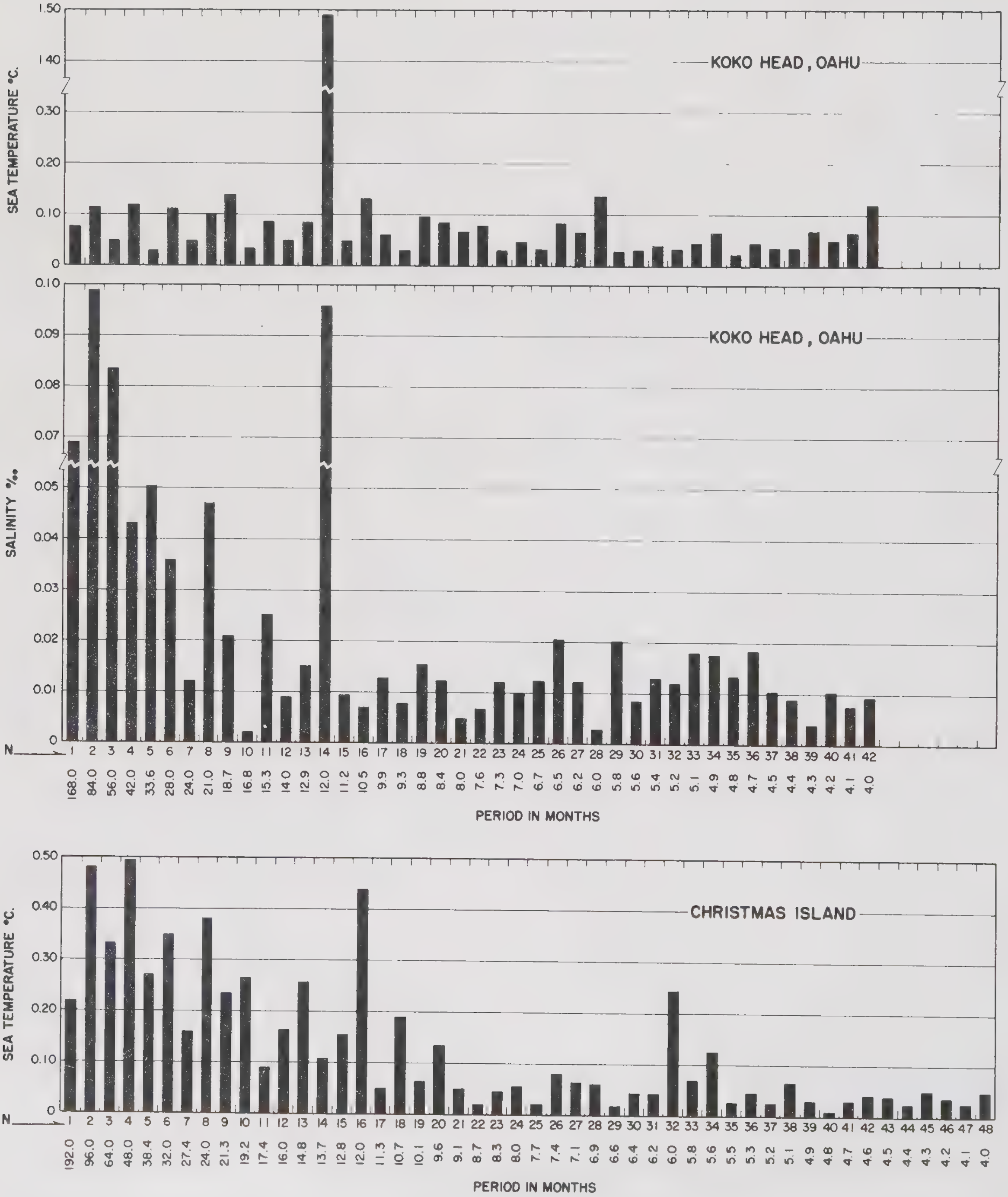

FIGURE 4.—Spectra of the long-term harmonic functions for Koko Head temperatures, 1956-69, Koko Head salinities, 1956-69, and Christmas Island temperatures, 1954-69.

suming that temperature and salinity samples are of Koko Head quality, then for a resolution of 1 month, weekly sampling is sufficient. Occasionally, however, a scheduled sample is not taken or an erroneous value must be eliminated. In such cases sampling gaps would become too large for the desired resolution. Undesirable sampling gaps can be avoided by doubling the minimum sampling frequency.

The simplicity and economy of deriving harmonic functions by computer are of practical value, particularly in the analysis of data sampled automatically. By this method large quantities of data can be brought into useful form rapidly.

The results of this paper, based on manual sampling, are useful in the investigations of changes with a duration of more than 1 month. Automated sampling would broaden the spectrum and permit analyses of shorter term variations such as diurnal changes, changes of tidal period, and other changes with durations of less than 1 month.

Automated sampling would also improve the quality of data since instruments can be placed in locations where undesirable variability is minimized and where manual sampling is difficult. At Koko Head, for example, samples are obtained from an exposed rock ledge where the island effects on the temperature and salinity are small. At Christmas Island, however, the sampling site is convenient and the best obtainable for manual sampling, but it is not the best in terms of monitoring open-ocean temperatures. This shortcoming is often also the case when temperatures and salinities are measured at tide stations located in protected bays or harbors.

The value of regularly monitoring the sea-surface temperatures and salinities has been demonstrated in many instances. For example, empirical relations between Koko Head temperatures and salinities and the availability of skipjack tuna to the Hawaiian fishery have been demonstrated (Seckel, 1963). Bjerknes (1969) has shown the relationship between anomalously high equatorial sea-surface temperatures using primarily Canton Island observations, and the intensification of the North Pacific westerlies and trades. This relationship must, in turn, affect temperatures and salinities in the North Pacific.

In view of these factors, serious consideration should be given to the establishment of automated sampling stations at selected islands in the Pacific. The derivation of harmonic functions, as demonstrated in this paper, would make reduction of data into usable form simple and economical and so facilitate the study of processes which govern the climate in both ocean and atmosphere.

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APPENDIX A

Sea-surface temperatures and salinities, Koko Head, Oahu, 1956-69: Phase angles and coefficients for harmonic functions

$$S = K + bt + \sum_{n=1}^{k} C_n \cos\omega(nt - \alpha_n) ,$$

$$\omega = \frac{2\pi}{365} \text{ days}^{-1} ,$$

t is the time in days beginning with the first day in each year.

Appendix A Table 1.—Phase angles and coefficients for sea-surface temperatures, Koko Head, 1956-69.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1956	73.88	69.97	10.42	-49.85	52.41	-25.23	70.98	-87.01	-55.97	19.33	-75.22	-52.34	46.35
1957	76.76	-72.88	30.75	58.99	8.81	-38.20	35.79	73.88	47.14	15.87	-36.68	-16.51	-8.30
1958	62.38	-6.51	-54.94	48.26	-34.27	-45.62	-51.72	-71.25	-46.58	-51.12	-10.61	-2.52	3.53
1959	65.59	-49.40	8.61	-1.48	56.56	-5.01	-70.18	17.77	71.89	-16.60	-27.85	-66.12	-50.78
1960	64.16	74.63	-62.69	37.38	-23.54	16.29	-89.39	23.77	-52.95	32.76	54.93	24.86	74.57
1961	53.19	15.31	-22.50	7.72	39.01	16.65	-51.44	-67.83	-2.26	49.83	88.27	-35.38	27.19
1962	66.15	-74.11	80.89	66.44	-7.78	-13.61	51.28	88.26	20.81	-30.04	29.78	41.65	-26.88
1963	63.76	-68.73	38.52	-27.45	-63.66	79.24	70.43	8.76	27.22	18.36	-76.61	35.19	-25.46
1964	73.31	-23.47	15.92	-57.15	-83.11	54.99	61.66	54.83	48.58	-0.50	51.76	3.89	-85.70
1965	64.85	45.82	-83.31	81.93	40.40	87.16	1.79	4.19	-21.73	-57.28	58.34	27.01	-90.88
1966	72.24	85.17	-29.44	82.13	-85.83	10.42	8.38	31.25	-0.28	-55.09	-24.99	65.54	-64.62
1967	60.48	66.72	-70.68	-9.91	83.89	84.03	-81.16	69.38	-9.63	-62.49	-84.89	-59.30	61.41
1968	65.18	71.07	-5.56	-19.37	26.00	-1.69	9.55	-41.85	-4.66	70.29	32.63	-19.50	-50.35
1969	58.78	-16.32	-68.76	90.78	49.97	12.98	89.93	40.17	-0.78	43.89	-88.96	-54.80	76.11
MEAN	66.13	62.61	-34.59	-9.48	68.75	40.82	29.88	86.20	-16.08	23.05	79.63	19.30	-87.99

APPENDIX A TABLE 1.—Phase angles and coefficients for sea-surface temperatures, Koko Head, 1956-69.—*Continued.*

			AMPLITUDES												
			N-VALUES												
YEAR	K	b	1	2	3	4	5	6	7	8	9	10	11	12	13
1956	24.2857	0.0014	-1.1174	-0.1340	-0.1099	-0.0633	0.0255	-0.1008	-0.0407	0.0206	0.0575	0.0346	-0.0565	0.0313	-0.0228
1957	25.1584	-0.0039	-2.0983	0.3004	-0.2188	0.0195	-0.1006	-0.0499	-0.0256	-0.1151	-0.0761	-0.0508	0.0691	0.0278	0.0400
1958	24.2433	0.0011	-1.4988	-0.1047	-0.2459	-0.0062	-0.0965	0.0225	-0.0385	-0.0154	0.0513	0.1033	-0.0374	-0.0878	-0.0477
1959	24.3697	0.0008	-1.5707	-0.2354	-0.3358	0.0470	0.1414	-0.1173	-0.0240	0.0239	0.0798	0.0968	-0.0969	0.0389	-0.0391
1960	24.3239	0.0008	-1.4963	-0.1570	-0.1641	0.0825	0.0383	-0.0437	0.0810	-0.0558	0.1175	0.0393	0.0931	-0.0677	0.1034
1961	24.7453	0.0006	-1.0587	-0.4112	-0.1832	0.1314	0.0498	0.1401	-0.0574	0.1761	0.1798	0.1026	0.1073	-0.1105	-0.0403
1962	24.7987	-0.0014	-1.4437	0.2802	0.0761	0.0502	-0.1250	0.1465	0.0561	-0.0798	0.0590	-0.0587	0.0302	0.0352	0.1037
1963	24.3471	0.0019	-1.4430	-0.1124	-0.1025	0.0501	0.0916	-0.0979	0.1870	0.0645	-0.1092	-0.0450	-0.0409	0.0344	0.0424
1964	24.7972	-0.0008	-1.0946	-0.0931	0.0691	0.1611	-0.0573	-0.0956	-0.0675	-0.1461	0.0639	-0.1162	0.0872	-0.0194	-0.0702
1965	24.8006	-0.0003	-1.6891	-0.2896	-0.3339	0.1715	0.1857	0.2120	0.1332	0.1040	0.0290	0.0596	0.0518	-0.0716	0.0622
1966	25.0047	-0.0014	-1.9152	-0.4056	-0.0944	-0.1330	0.0300	-0.1687	0.0236	0.0548	0.0825	-0.0161	0.0254	-0.0170	0.0253
1967	25.2850	-0.0008	-1.8725	-0.2850	-0.3005	-0.1125	-0.0966	-0.2437	0.1082	-0.0694	0.0794	-0.0341	0.0586	0.0555	-0.0572
1968	24.8546	0.0028	-1.5364	-0.2820	-0.2155	-0.0568	-0.0194	-0.0275	0.1192	-0.1263	0.0787	-0.0445	-0.0137	0.0294	-0.0817
1969	24.7701	0.0003	-1.3374	0.2035	-0.0760	-0.1235	0.1544	0.1096	0.1056	-0.0626	0.0594	0.1396	-0.1064	-0.0373	-0.0016
MEAN	24.6989	0.0001	-1.5040	-0.1458	-0.1291	0.0147	0.0220	-0.0164	0.0215	-0.0335	0.0461	0.0098	0.0324	-0.0135	-0.0013

APPENDIX A TABLE 2.—Phase angles and coefficients for sea-surface salinities, Koko Head, 1956-69.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1956	-14.52	-68.27	-89.13	-4.08	52.05	15.36	16.54	-2.09	-40.95	62.40	24.44	-7.01	-8.85
1957	-25.52	67.90	6.11	22.47	4.85	-25.00	-8.60	-19.40	28.27	-82.38	73.57	83.14	34.59
1958	25.99	46.89	57.99	50.30	15.25	-88.16	17.82	-10.99	20.65	-34.78	43.80	-31.33	-5.52
1959	-57.46	-68.08	18.94	-71.46	59.29	-35.64	-64.98	-19.12	-72.96	71.02	3.20	-8.24	28.66
1960	15.99	-61.03	81.05	56.42	-14.00	43.21	-58.49	-64.87	-87.20	62.22	71.57	4.93	-16.77
1961	-17.27	48.97	45.52	-26.18	2.69	13.58	2.15	-50.58	-38.94	82.68	-85.76	70.83	72.92
1962	-37.91	35.77	-1.00	-88.77	23.96	-32.29	-56.02	43.47	21.90	-52.99	24.88	-39.69	0.0
1963	17.33	-33.19	-66.85	53.84	13.09	-61.03	86.91	-72.22	12.17	2.06	-56.52	27.79	-39.95
1964	28.39	-19.79	-82.91	-82.99	53.70	-69.42	55.05	51.23	-17.95	8.29	-67.42	-80.98	-1.92
1965	-39.50	1.54	-49.50	-29.90	-31.57	-81.95	9.24	1.57	-56.55	90.65	42.78	-22.53	9.48
1966	-51.26	10.69	59.98	14.96	-10.51	78.69	26.93	-21.00	-86.73	30.96	10.93	-40.71	64.32
1967	-50.66	-58.57	35.70	38.98	-76.06	-77.32	-70.26	-26.09	17.82	-57.29	-13.46	26.17	44.48
1968	12.29	85.76	80.38	-11.84	-1.90	-31.29	-19.27	-49.39	-5.37	43.75	-66.43	70.00	18.69
1969	-9.16	30.08	30.65	-63.98	-47.50	47.99	74.49	66.13	-85.89	48.21	84.68	-58.03	-60.81
MEAN	-11.17	47.12	63.72	46.06	26.70	29.49	39.79	-16.95	-79.12	-76.28	-75.40	13.10	-5.70

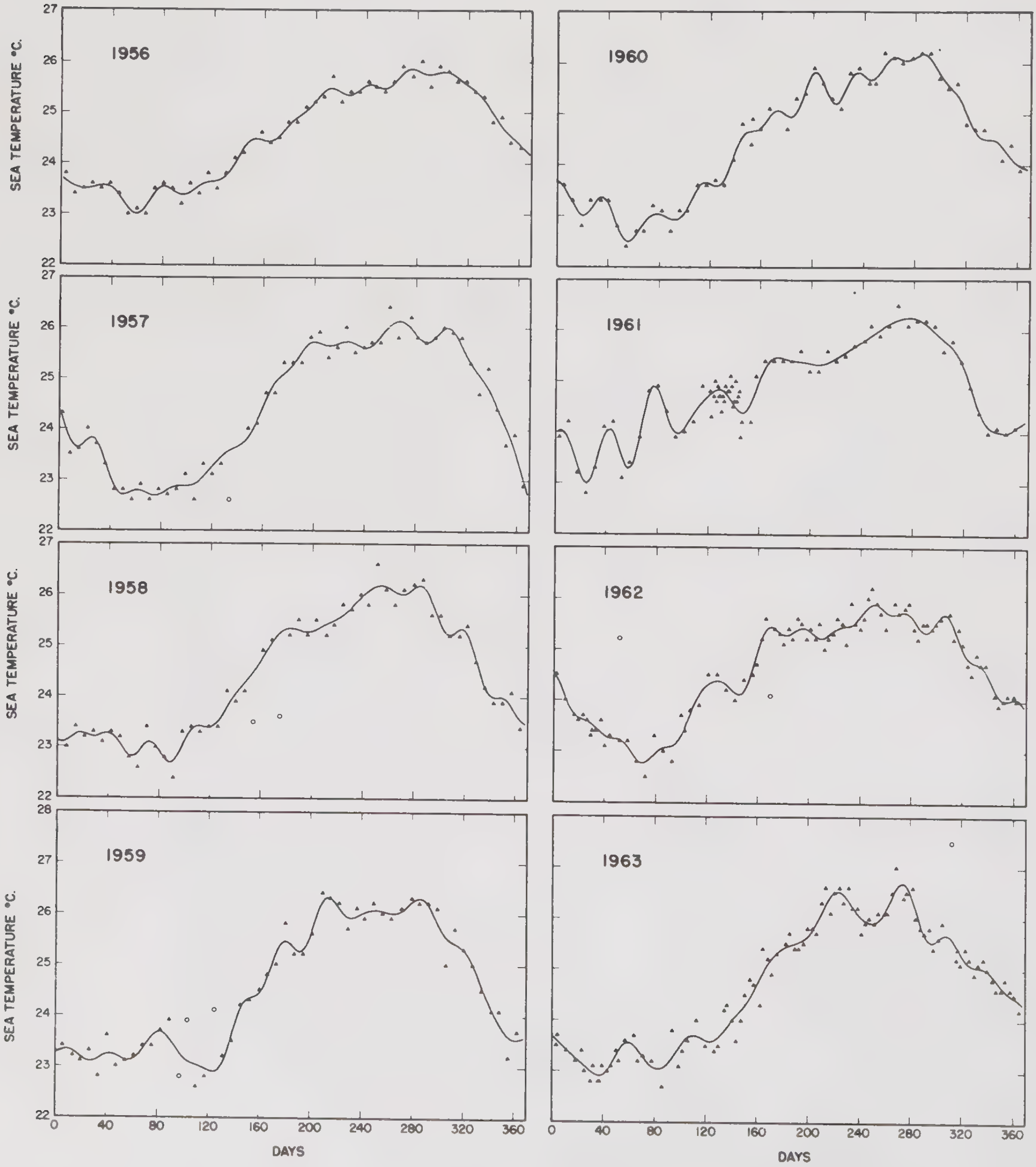
APPENDIX A TABLE 2.—Phase angles and coefficients for sea-surface salinities, Koko Head, 1956-69.—*Continued.*

			AMPLITUDES												
			N-VALUES												
YEAR	K	b	1	2	3	4	5	6	7	8	9	10	11	12	13
1956	34.8727	-0.0001	0.1261	-0.0420	-0.0164	-0.0071	0.0038	0.0099	0.0043	0.0167	-0.0176	-0.0258	0.0240	-0.0133	0.0270
1957	34.9345	0.0006	0.0604	-0.0544	-0.0305	-0.0029	0.0407	0.0242	0.0183	-0.0156	0.0195	-0.0079	-0.0127	0.0122	-0.0037
1958	34.9491	0.0004	0.1650	0.0324	0.0412	0.0088	0.0262	-0.0244	0.0063	0.0213	0.0244	-0.0130	-0.0292	0.0160	-0.0042
1959	35.2530	-0.0018	0.1996	0.2016	0.0884	0.0168	-0.0140	0.0120	-0.0272	-0.0340	-0.0271	0.0179	0.0254	-0.0191	0.0106
1960	34.8357	0.0000	0.1089	-0.0434	-0.0269	-0.0287	0.0239	0.0188	-0.0380	0.0378	-0.0373	-0.0198	-0.0187	0.0283	-0.0172
1961	34.8545	0.0001	0.1147	0.0368	0.0375	-0.0172	-0.0194	-0.0324	0.0162	-0.0191	-0.0179	-0.0177	0.0117	0.0064	-0.0151
1962	34.9396	0.0001	0.1084	-0.0230	-0.0116	0.0211	0.0035	0.0190	0.0254	0.0076	-0.0103	0.0106	-0.0051	0.0055	-0.0064
1963	34.9780	0.0001	0.1388	0.0067	-0.0164	-0.0371	0.0161	-0.0111	-0.0215	0.0162	0.0226	-0.0113	0.0197	0.0122	-0.0072
1964	34.9727	0.0001	0.1178	-0.0503	-0.0503	-0.0416	0.0209	-0.0158	0.0394	-0.0022	-0.0174	0.0316	-0.0025	-0.0142	0.0272
1965	34.9953	-0.0010	0.1566	-0.0564	0.0477	0.0412	0.0056	0.0163	0.0328	-0.0185	0.0356	0.0195	-0.0188	0.0331	0.0252
1966	34.8927	0.0006	-0.0401	-0.0131	0.0156	0.0271	0.0083	-0.0177	-0.0011	-0.0088	-0.0077	0.0161	0.0043	0.0084	-0.0114
1967	35.0184	-0.0009	0.1037	-0.0109	-0.0366	0.0248	-0.0310	-0.0417	-0.0368	-0.0184	-0.0169	0.0167	0.0091	0.0237	0.0179
1968	34.7135	-0.0006	0.1219	0.0424	0.0134	-0.0306	-0.0245	0.0191	0.0160	-0.0055	-0.0195	0.0044	0.0147	0.0050	-0.0022
1969	34.5912	0.0007	0.0821	0.0190	-0.0441	-0.0157	0.0044	-0.0243	-0.0200	0.0172	-0.0054	-0.0222	-0.0044	0.0103	0.0052
MEAN	34.9143	-0.0001	0.0972	-0.0051	0.0071	-0.0013	0.0064	0.0013	0.0070	-0.0026	-0.0065	0.0022	0.0073	0.0067	0.0040

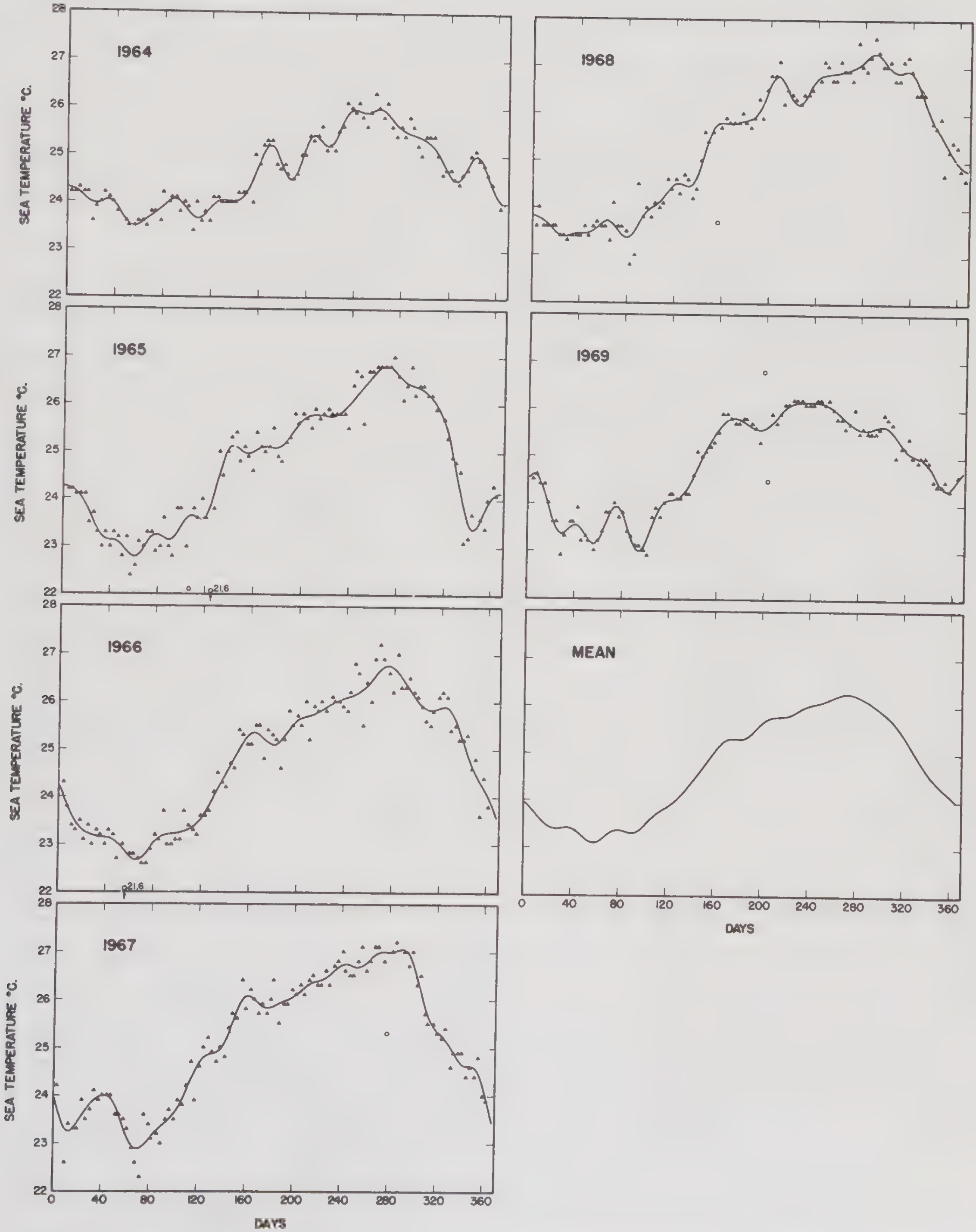
APPENDIX B

Sea-surface temperatures and salinities, Koko Head, Oahu, 1956-69: Fitted curves with observed values for each year.

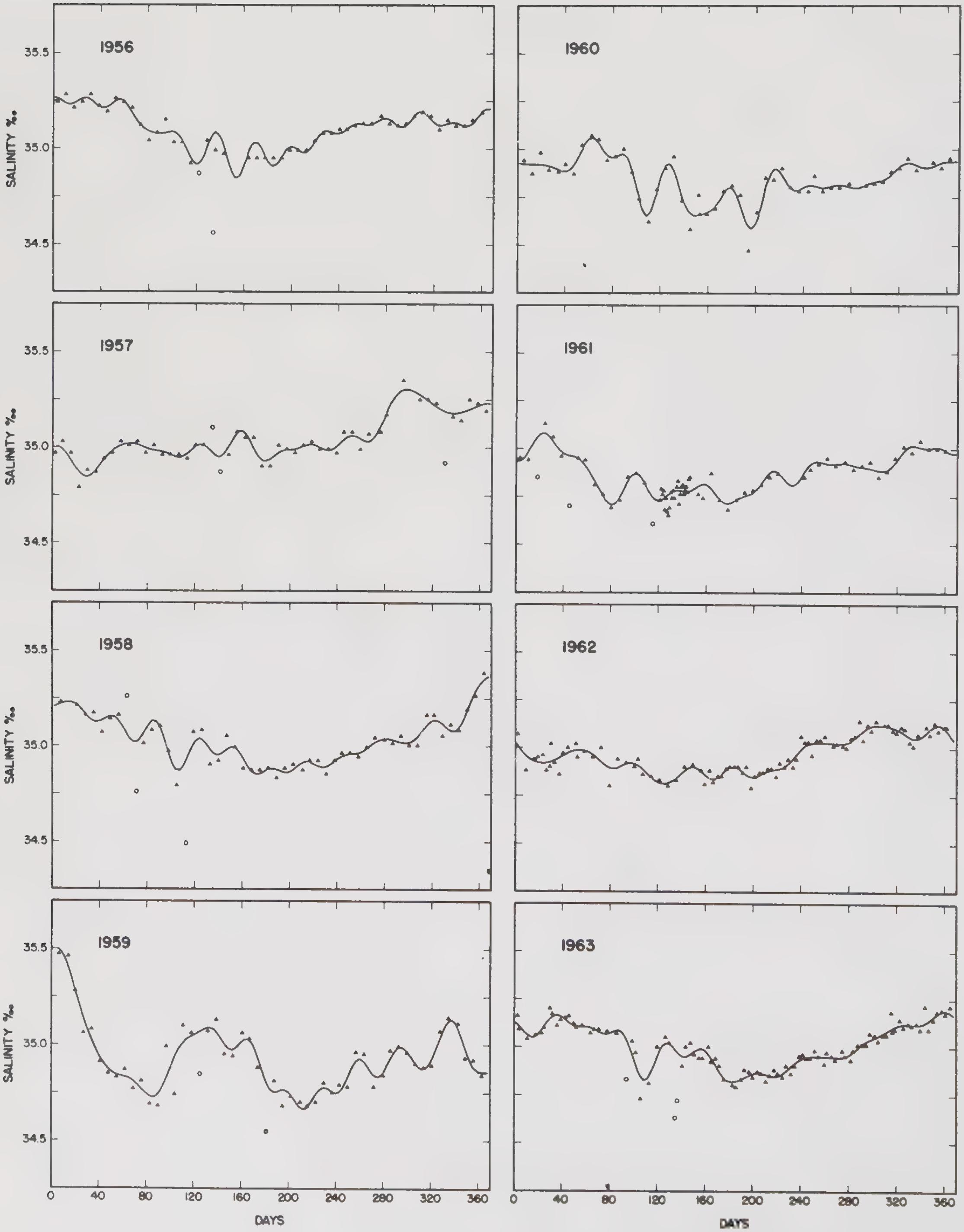
Note: Circled observations have not been used in the harmonic analysis.



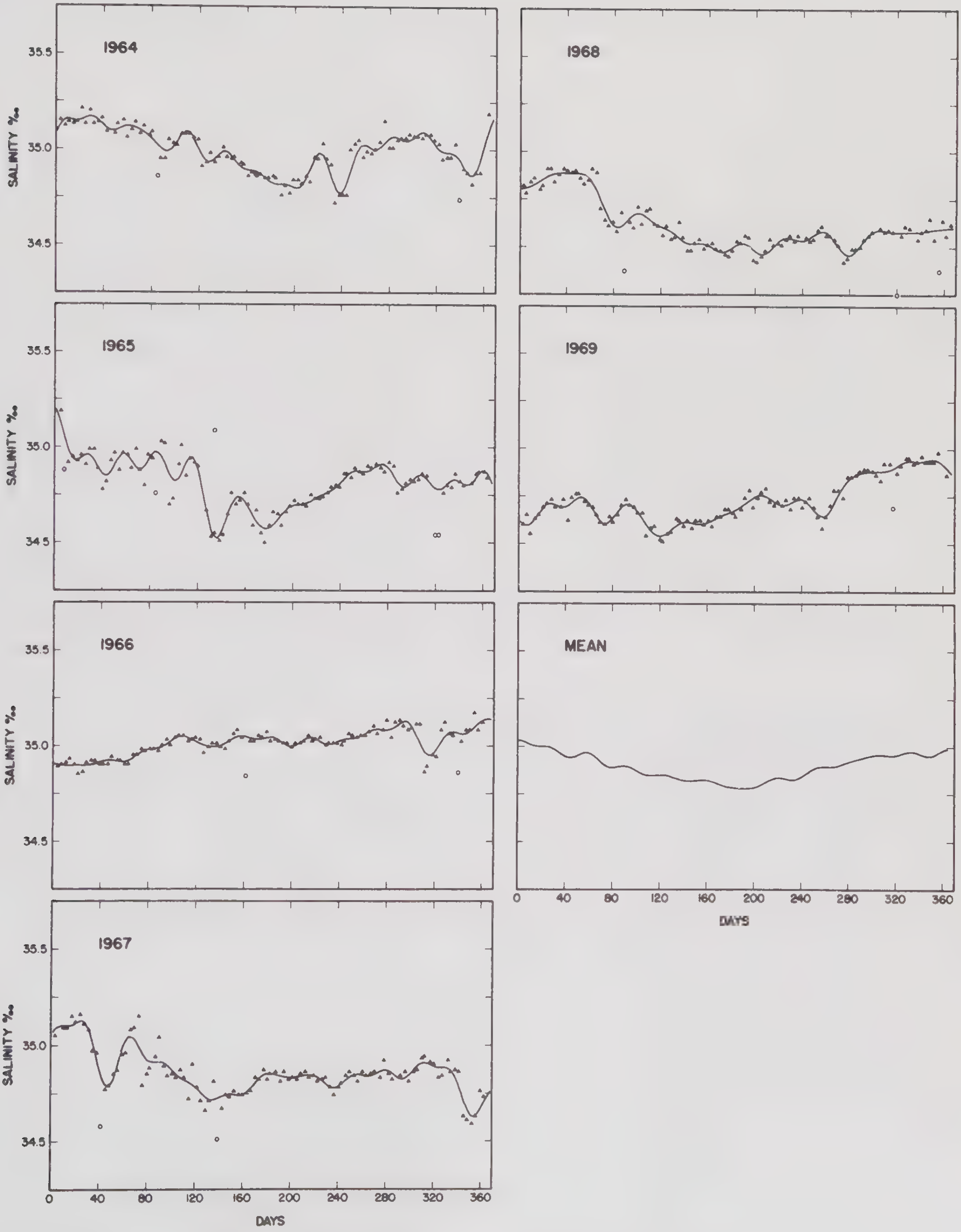
APPENDIX B FIGURE 1.—Sea-surface temperatures, Koko Head, 1956-69.



APPENDIX B FIGURE 1.—Sea-surface temperatures, Koko Head, 1956-69.—*Continued.*



Appendix B Figure 2.—Sea-surface salinities, Koko Head, 1956-69.



APPENDIX B FIGURE 2.—Sea-surface salinities, Koko Head, 1956-69—*Continued.*

APPENDIX C

Sea-surface temperatures, Christmas Island, 1954-69. Phase angles and coefficients for harmonic functions for each quarter of each year:

Days 1 to 120 = First quarter,
91 to 210 = Second quarter,
181 to 300 = Third quarter,
271 to 390 = Fourth quarter, extending 25 days into new year,

$$S = K + bt + \sum_{n=1}^{k} C_n \cos\omega(nt - \alpha_n) \ ,$$

$$\omega = \frac{2\pi}{120} \text{ days}^{-1} \ ,$$

t is the time in days beginning with the first day of each quarter.

Note: Mean values do not include phase angles and coefficients for the third and fourth quarters of 1967.

APPENDIX C TABLE 1.—Phase angles and coefficients for sea-surface temperatures, Christmas Island, 1954-69.

PHASE ANGLES IN DAYS

		N-VALUES						
YEAR	QU.	1	2	3	4	5	6	7
1954	1	29.96	-14.98	0.68	22.60	-16.29	0.45	-28.43
	2	21.92	24.40	-25.77	15.21	23.02	24.75	8.06
	3	-19.46	21.45	-25.73	-10.27	-14.81	-6.52	-20.70
	4	-15.22	27.64	6.23	-9.84	25.21	27.55	-26.39
1955	1	-25.04	-14.36	-19.66	-25.05	10.26	1.57	-17.43
	2	-1.34	-22.96	16.15	-12.62	-27.83	-6.10	24.53
	3	-28.76	23.27	29.69	-21.77	-18.26	28.12	10.11
	4	-5.04	-11.73	-11.08	5.52	9.94	-2.89	-1.09
1956	1	-15.33	29.40	18.77	24.08	27.16	17.61	-20.53
	2	25.55	29.94	-23.88	27.18	-22.20	-10.40	-16.16
	3	-26.54	21.39	-22.54	13.46	20.29	29.39	-17.29
	4	-28.99	16.56	-15.87	-0.61	6.14	-27.68	1.48
1957	1	-20.33	9.65	-3.33	-13.39	-22.18	24.07	4.11
	2	12.45	3.80	-21.56	22.60	5.19	18.04	16.55
	3	12.50	-8.47	27.08	22.42	5.63	4.72	-24.37
	4	1.99	-11.91	-1.14	15.68	5.08	-17.77	-21.22
1958	1	-15.56	-9.55	16.21	-19.82	-16.02	-9.08	8.91
	2	-25.92	-8.31	-7.41	26.09	-26.16	-28.63	17.52
	3	17.11	-4.98	25.83	9.96	6.39	-15.05	-24.35
	4	-25.45	16.23	-11.73	19.38	7.25	16.83	20.96
1959	1	-11.25	18.21	25.30	27.40	2.42	-3.45	-27.76
	2	-4.58	-18.05	-2.17	-6.57	15.76	-29.98	28.66
	3	-13.92	-7.90	26.00	-0.14	15.14	3.09	21.42
	4	-25.63	-23.22	-13.08	18.13	-10.51	-22.26	28.72
1960	1	-21.36	3.16	-22.67	15.60	-1.99	22.75	21.91
	2	14.95	-26.09	18.68	6.43	23.12	-22.78	28.33
	3	21.14	17.18	10.04	7.87	6.28	20.84	-2.55
	4	-0.89	0.26	-28.94	9.46	17.99	23.48	-26.06
1961	1	-4.50	2.29	14.03	9.01	9.50	-26.75	14.56
	2	-9.38	-18.74	15.60	10.81	5.59	-18.31	-27.53
	3	-27.87	-27.65	27.26	26.89	21.47	-10.55	-13.26
	4	-19.95	-17.14	-3.05	0.39	-13.80	-7.92	24.95
1962	1	10.13	-24.96	-16.24	29.64	4.40	16.34	-1.98
	2	-10.33	-1.79	27.51	28.58	-0.81	8.88	-15.25
	3	18.78	20.95	-6.12	-29.13	-2.99	-1.52	2.56
	4	29.70	7.75	14.37	-13.15	-25.15	-4.47	13.65
1963	1	18.62	14.96	21.66	21.78	-21.72	-8.72	-19.16
	2	-25.86	-23.08	-21.84	-25.95	-12.90	-7.23	-3.15
	3	27.97	-11.92	17.92	-10.01	20.37	-9.25	15.06
	4	5.53	-27.74	-4.23	12.23	13.77	6.00	-14.49
1964	1	10.51	23.82	-4.95	-11.60	-22.13	13.52	9.47
	2	29.78	-24.66	11.64	-19.75	22.21	-13.85	-22.39
	3	3.66	-21.54	13.24	5.89	-17.78	16.09	6.84
	4	9.57	-19.61	-22.27	-11.16	-12.19	-18.46	-4.51
1965	1	-12.81	22.40	-29.54	24.56	25.12	16.28	-23.00
	2	-16.03	-23.97	-7.39	-19.45	2.93	-11.03	1.10
	3	28.09	-13.92	12.10	-9.87	6.09	14.42	-23.32
	4	-10.42	20.99	27.57	29.48	-18.90	17.82	-18.83
1966	1	-2.72	-22.51	-8.68	9.75	-10.62	-6.62	29.58
	2	29.77	26.12	4.26	21.28	15.28	27.61	-22.03
	3	7.34	25.04	9.12	25.58	1.93	10.76	4.92
	4	8.34	0.12	-20.67	1.80	-28.17	3.39	26.99
1967	1	-22.45	14.34	-25.09	18.95	0.56	10.45	-20.67
	2	-8.36	-8.88	-1.88	-22.37	-24.08	16.60	21.27
	3	-29.90	-2.24	18.31	26.99	-16.01	9.55	-12.24
	4	-19.32	23.12	7.45	-6.85	-19.61	7.19	8.69
1968	1	-9.18	-10.65	23.64	-20.93	11.66	-20.43	-24.40
	2	-14.96	-23.53	13.31	-14.18	7.83	27.96	20.00
	3	-0.07	-22.76	5.17	5.55	-23.92	-10.81	-2.39
	4	27.65	-15.84	3.23	-21.90	-10.88	-24.36	6.48
1969	1	13.34	14.46	6.54	-17.39	7.54	6.63	-7.29
	2	8.02	-23.81	-20.76	26.56	-28.81	29.11	27.75
	3	22.54	11.28	11.96	25.05	-8.17	12.69	28.92
	4	-24.65	-0.88	-15.33	-12.66	-11.06	-13.66	4.95
MEAN	1	-14.97	-10.80	-22.92	-20.97	16.82	20.22	20.72
	2	9.25	11.74	20.56	15.71	28.30	-19.45	-9.57
	3	5.57	22.63	15.62	14.65	25.53	22.30	-25.12
	4	-4.77	-2.64	-27.75	-26.43	20.79	-26.95	10.88

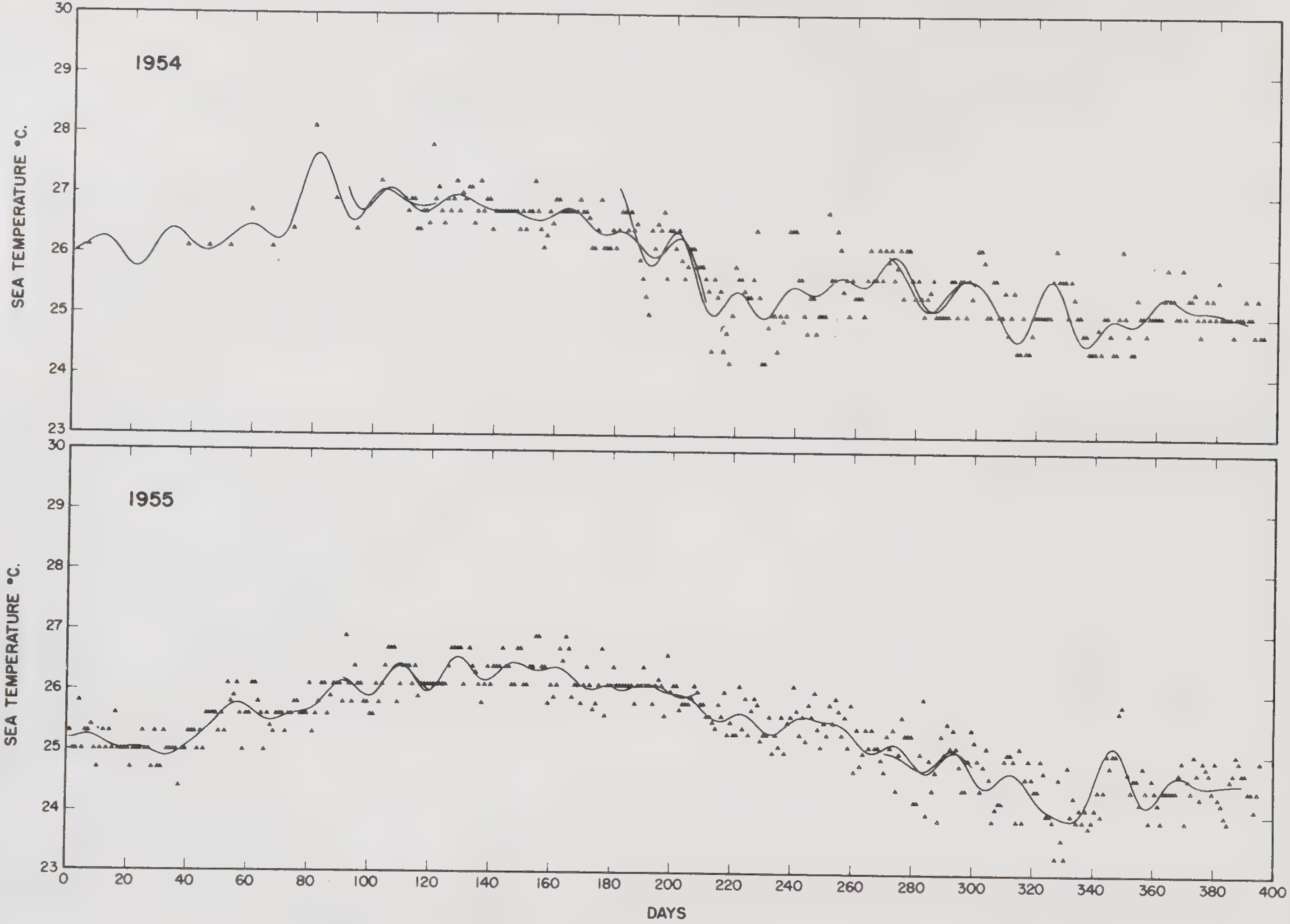
APPENDIX C TABLE 1.—Phase angles and coefficients for sea-surface temperatures, Christmas Island, 1954-69—*Continued.*

				AMPLITUDES						
				N-VALUES						
YEAR	QU.	K	b	1	2	3	4	5	6	7
1954	1	26.0740	0.0070	-0.2543	-0.1310	0.1609	-0.0772	-0.2829	0.0637	0.0743
	2	27.5957	-0.0169	-0.3583	-0.1443	0.1307	-0.1171	-0.1275	-0.1517	-0.0342
	3	26.4268	-0.0139	0.6131	0.0815	-0.0171	0.1382	0.2404	0.1808	-0.1111
	4	25.6919	-0.0090	0.2918	-0.1571	-0.0880	0.2517	0.1746	-0.1001	-0.0949
1955	1	25.1633	0.0067	0.2697	0.1614	-0.0873	0.1008	-0.0360	-0.0632	-0.0698
	2	26.2916	-0.0017	-0.1687	0.0292	-0.0565	-0.0347	0.0635	0.1000	0.1044
	3	26.1027	-0.0107	-0.0046	0.1350	-0.0375	-0.0218	0.0858	-0.0284	-0.0917
	4	24.8187	-0.0041	0.2259	-0.1449	0.1578	-0.1789	0.1836	0.0816	-0.0946
1956	1	24.3949	0.0183	0.4678	-0.1493	-0.0999	0.1311	-0.1107	-0.0674	0.0277
	2	27.7890	-0.0174	-0.4323	-0.2228	0.1648	-0.1209	0.1879	0.0861	0.0232
	3	27.0093	-0.0139	0.5433	-0.1689	0.1687	-0.1784	-0.1535	0.1829	0.0787
	4	26.1278	-0.0049	0.1022	0.0890	-0.1479	-0.0249	-0.0544	0.2481	-0.0168
1957	1	25.4577	0.0176	0.3612	0.1892	0.1458	0.1574	0.1045	0.0540	0.0693
	2	27.7558	0.0025	-0.2169	-0.4098	0.1621	-0.0802	-0.1359	0.2288	-0.1088
	3	27.6226	0.0008	0.4254	0.0970	0.0939	-0.1184	-0.2340	-0.1508	-0.1202
	4	28.0288	0.0066	-0.5153	0.0870	-0.2655	-0.1550	0.0453	0.2115	0.1495
1958	1	28.6567	-0.0050	0.1989	0.1052	0.0983	0.0407	0.0531	-0.0732	-0.0469
	2	28.2124	-0.0091	-0.2768	-0.0700	-0.0795	-0.0835	-0.1346	-0.0783	0.1074
	3	26.6129	0.0	0.3456	-0.1571	0.2536	0.0694	-0.1207	0.0260	0.0474
	4	26.2684	0.0066	-0.2862	0.0679	0.1955	0.1226	0.0867	-0.0855	0.0184
1959	1	26.8512	0.0025	0.3797	-0.3106	-0.2379	-0.1429	0.0562	-0.0545	0.0838
	2	27.8849	-0.0132	-0.2731	-0.1508	-0.1839	-0.1429	-0.0674	-0.0819	0.0641
	3	26.3895	-0.0025	0.5706	0.4088	-0.2084	-0.1502	-0.1315	-0.0472	-0.0216
	4	26.7237	-0.0091	-0.1536	-0.2531	-0.2372	-0.2151	0.1113	0.1418	-0.0299
1960	1	25.6504	0.0042	0.4722	0.0679	0.1461	0.1082	0.0721	-0.0691	0.0460
	2	26.9858	-0.0025	-0.3299	0.1787	-0.1260	-0.0797	0.0321	-0.0404	-0.0377
	3	26.5916	-0.0033	0.3107	0.1345	0.1430	-0.1676	-0.0941	0.0284	-0.0720
	4	26.0923	-0.0049	0.1670	-0.3080	0.1905	-0.1680	-0.0272	-0.1538	-0.1171
1961	1	25.3508	0.0109	0.3816	0.1665	0.0125	-0.1322	-0.1105	0.1068	0.1995
	2	26.7608	0.0025	-0.1900	-0.0611	-0.1699	-0.2098	0.1176	0.0254	0.0986
	3	26.5390	-0.0066	-0.4129	-0.2944	0.0796	0.0568	-0.1021	-0.1658	-0.0319
	4	25.3383	0.0016	-0.2387	0.1069	0.1592	-0.0197	0.1122	0.0896	0.0918
1962	1	24.9107	0.0168	0.1042	-0.2920	0.2226	0.0317	0.0329	0.1702	-0.0358
	2	26.5159	0.0033	-0.2921	-0.2701	-0.1616	0.1077	-0.0996	-0.1532	0.1131
	3	26.9093	-0.0139	-0.2714	0.1472	-0.1661	-0.0770	0.0532	0.0728	-0.0359
	4	25.6078	-0.0090	-0.2539	0.2136	0.0877	0.0963	-0.0275	-0.0509	-0.0641
1963	1	24.5106	0.0202	-0.1137	-0.0707	0.1670	0.0588	0.1332	-0.0370	-0.2257
	2	27.3700	-0.0033	0.5749	0.3627	0.3065	0.1391	0.1594	0.0779	0.2440
	3	27.2705	0.0041	0.3865	-0.2983	0.0802	-0.1328	0.1014	0.1157	-0.0641
	4	27.6762	-0.0066	-0.0697	0.1280	0.0933	0.1408	0.0886	0.0388	0.0603
1964	1	26.7596	-0.0025	0.4138	-0.0692	0.0988	0.1046	-0.0882	-0.0860	-0.0658
	2	26.2958	-0.0017	0.2579	-0.2425	-0.1394	0.0522	0.1147	0.0422	-0.0869
	3	26.0159	-0.0092	0.4285	-0.1814	0.1304	-0.0741	0.1106	0.0733	-0.1184
	4	24.8755	0.0033	0.1803	-0.1368	0.0999	0.1655	-0.0848	0.0989	-0.0299
1965	1	25.0849	0.0151	0.2248	-0.1215	0.0998	-0.0676	-0.1001	0.0939	-0.0430
	2	26.4776	0.0149	-0.2682	-0.2288	-0.1801	-0.0793	-0.0111	0.0295	-0.0471
	3	27.2809	0.0033	0.6393	0.1140	0.3702	0.2312	-0.2351	0.1376	-0.0732
	4	27.3759	0.0098	-0.7293	-0.2572	-0.0559	-0.1109	0.0830	-0.0606	-0.0654
1966	1	28.3584	-0.0076	-0.5145	0.1954	-0.2585	0.0741	-0.1413	0.1728	0.1227
	2	28.5148	-0.0198	-0.8788	-0.3261	0.0899	-0.0254	-0.0921	-0.1870	0.0975
	3	26.6145	-0.0041	0.4308	0.4345	0.2067	0.2310	0.2313	0.0932	0.1898
	4	27.2510	-0.0164	-0.8011	-0.0462	0.6174	0.1390	-0.1069	-0.0289	-0.2482
1967	1	25.3932	0.0076	0.3944	0.1627	0.2864	-0.0779	0.0240	-0.1438	0.0926
	2	26.4576	0.0066	-0.5433	-0.1618	-0.1932	-0.0712	-0.0620	0.0473	0.0553
	3	26.8336	-0.0044	0.1341	0.1093	0.0717	0.0649	-0.0896	-0.0822	0.0505
	4	27.8062	-0.0233	-0.0832	0.0851	0.0784	0.0593	0.0301	0.0046	0.0312
1968	1	25.1250	0.0033	0.5597	0.2691	-0.1413	0.2029	0.0708	0.0239	0.0730
	2	25.9567	0.0066	-0.1308	-0.1705	-0.2038	0.0706	0.0276	-0.1003	0.0172
	3	26.2971	0.0057	0.3013	0.0743	-0.1219	0.2030	0.1886	-0.2381	0.2042
	4	26.9967	0.0	0.1068	-0.0967	-0.1344	0.1499	-0.1181	-0.1165	0.0213
1969	1	26.4649	0.0168	0.1895	0.1321	-0.0869	-0.1854	0.0663	-0.0638	0.0926
	2	28.5357	-0.0165	-0.2815	0.3460	0.1314	-0.1603	0.1393	-0.1347	-0.1080
	3	27.0045	-0.0025	-0.0625	0.1304	-0.0853	-0.1166	-0.0388	0.1949	0.0671
	4	26.4789	0.0074	-0.2169	-0.0886	-0.1190	-0.1058	-0.1537	-0.0858	-0.0390
MEAN	1	25.8878	0.0082	0.2151	0.0484	0.0522	0.0285	-0.0074	-0.0107	0.0132
	2	27.2124	-0.0041	-0.1744	-0.0779	-0.0930	-0.0509	-0.0233	0.0283	0.0229
	3	26.7124	-0.0044	0.1770	0.0789	0.0498	-0.0071	-0.0629	0.0384	-0.0094
	4	26.3568	-0.0019	-0.0997	-0.0317	0.0509	0.0459	0.0341	0.0573	-0.0145

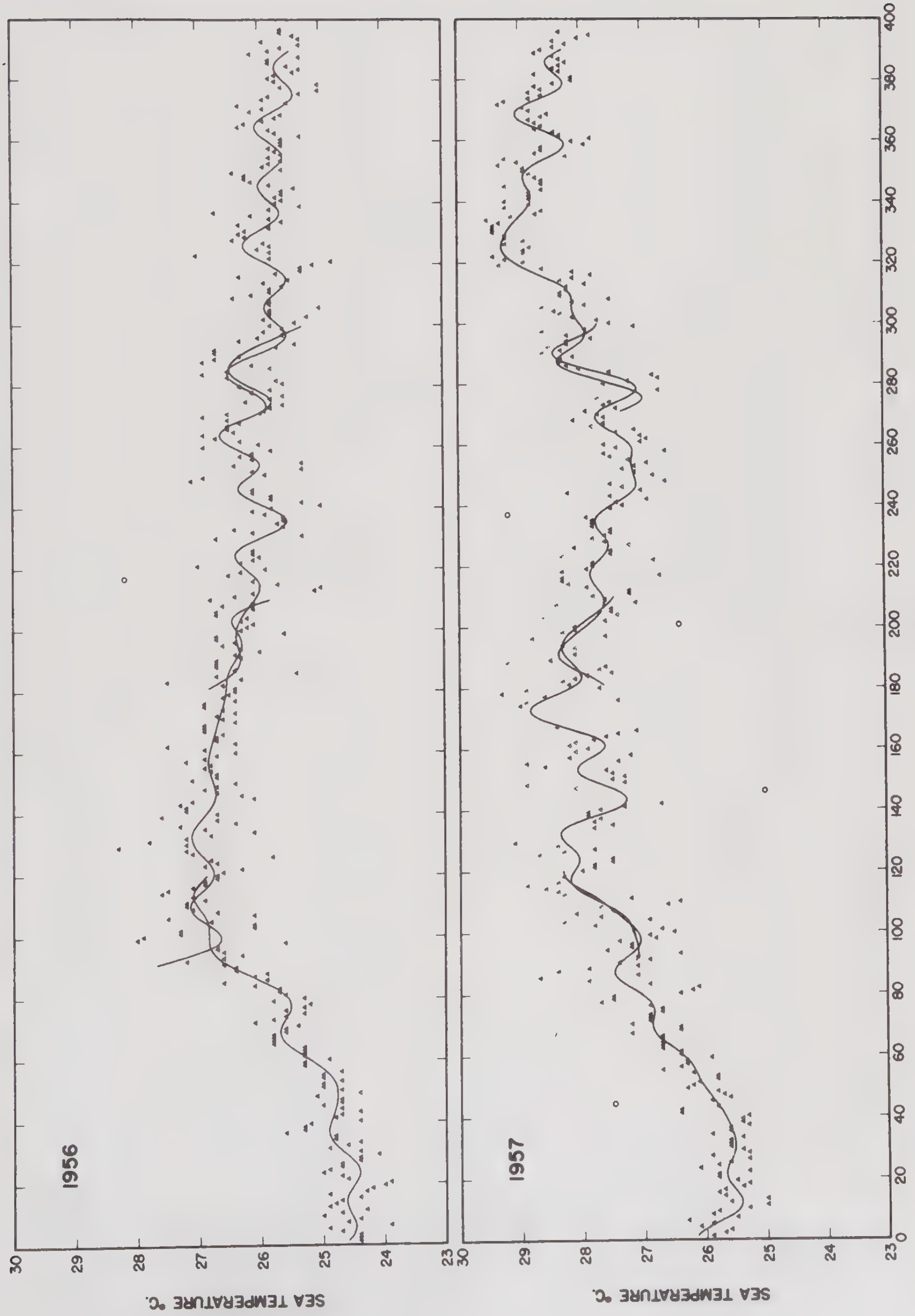
APPENDIX D

Sea-surface temperatures, Christmas Island, 1954-69: Fitted curves with observed values for each year.

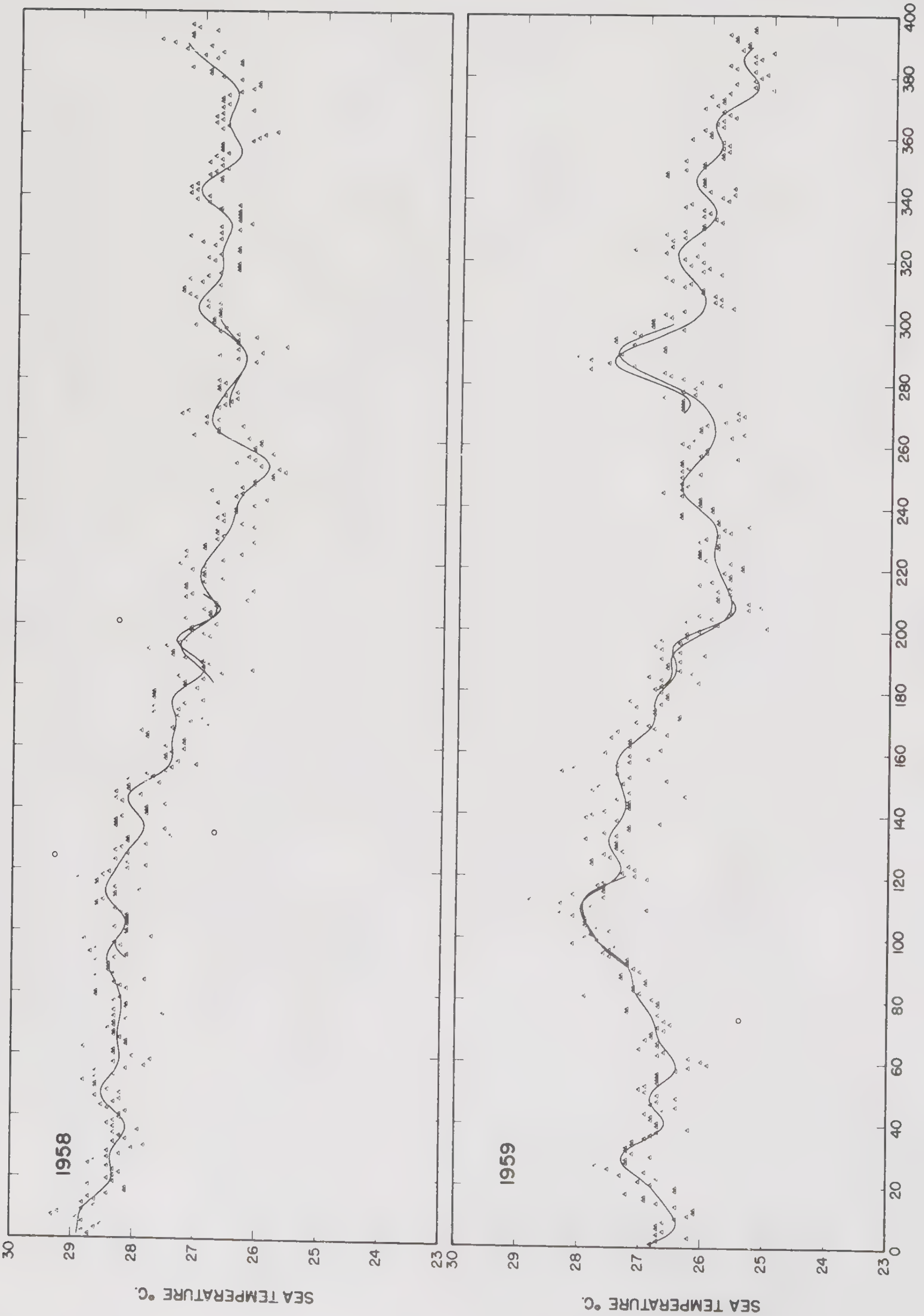
Note: Circled observations have not been used in the harmonic analysis.



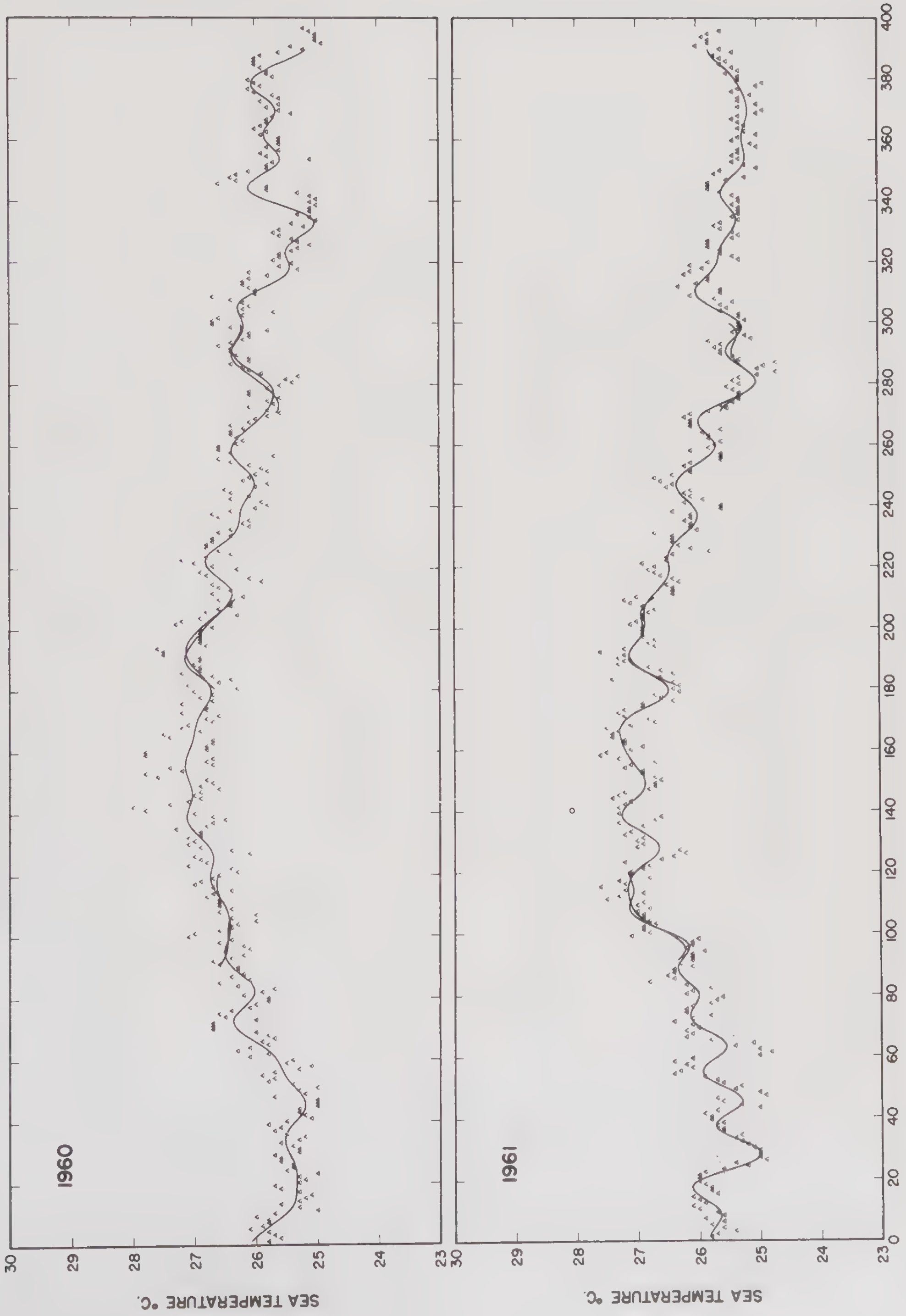
Appendix D Figure 1.—Sea-surface temperatures, Christmas Island, 1954-69.



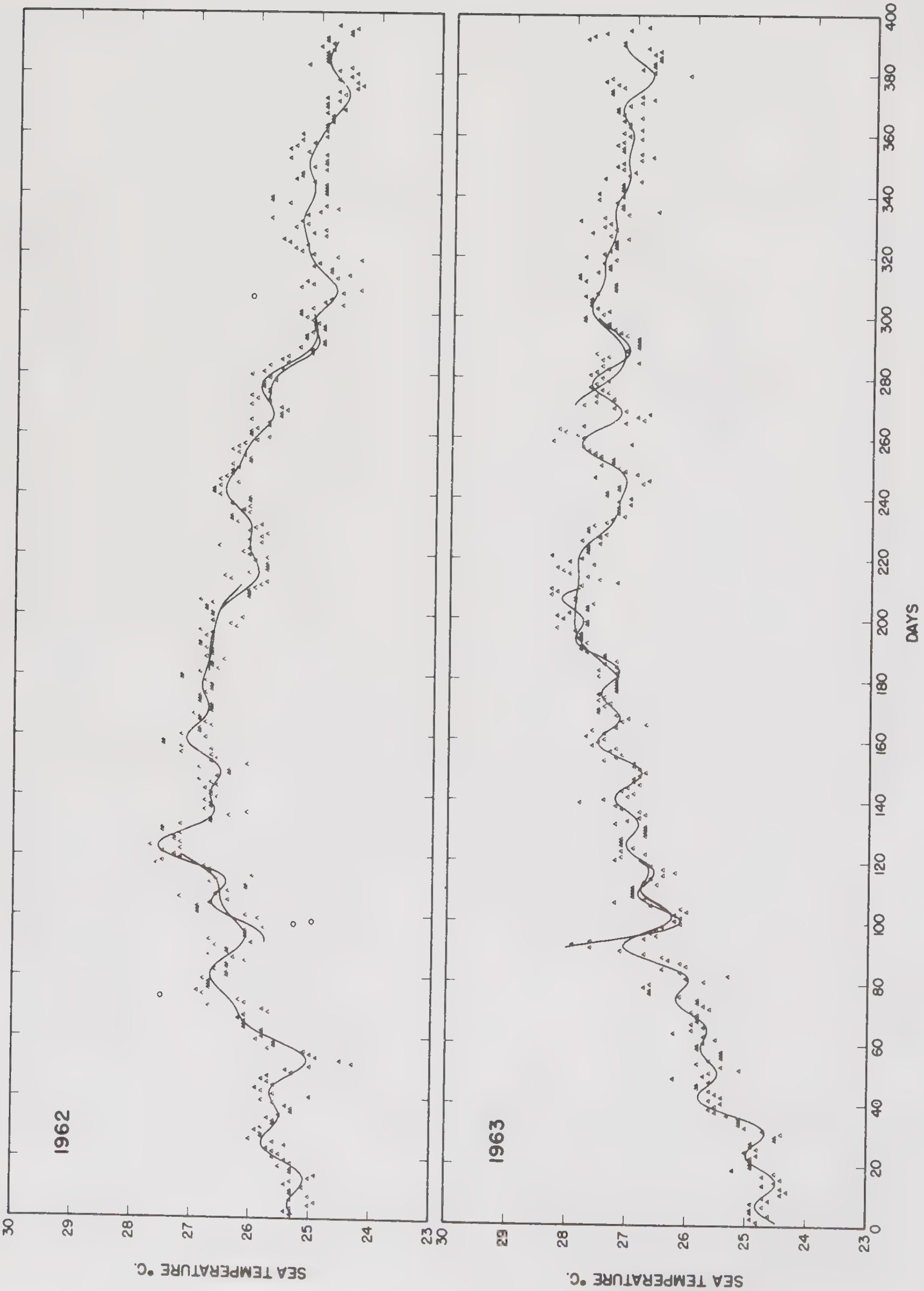
APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*



APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*



APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*



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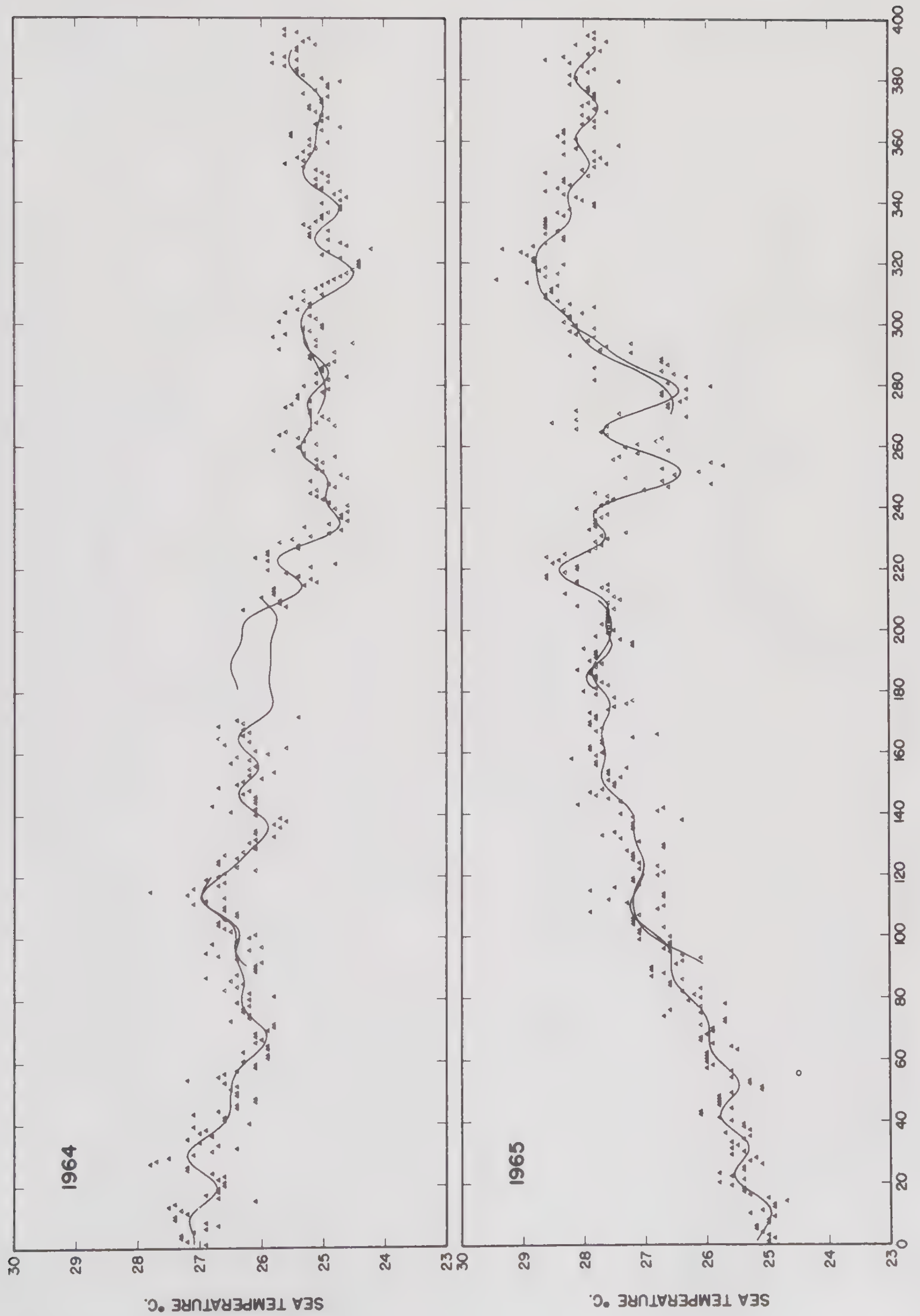
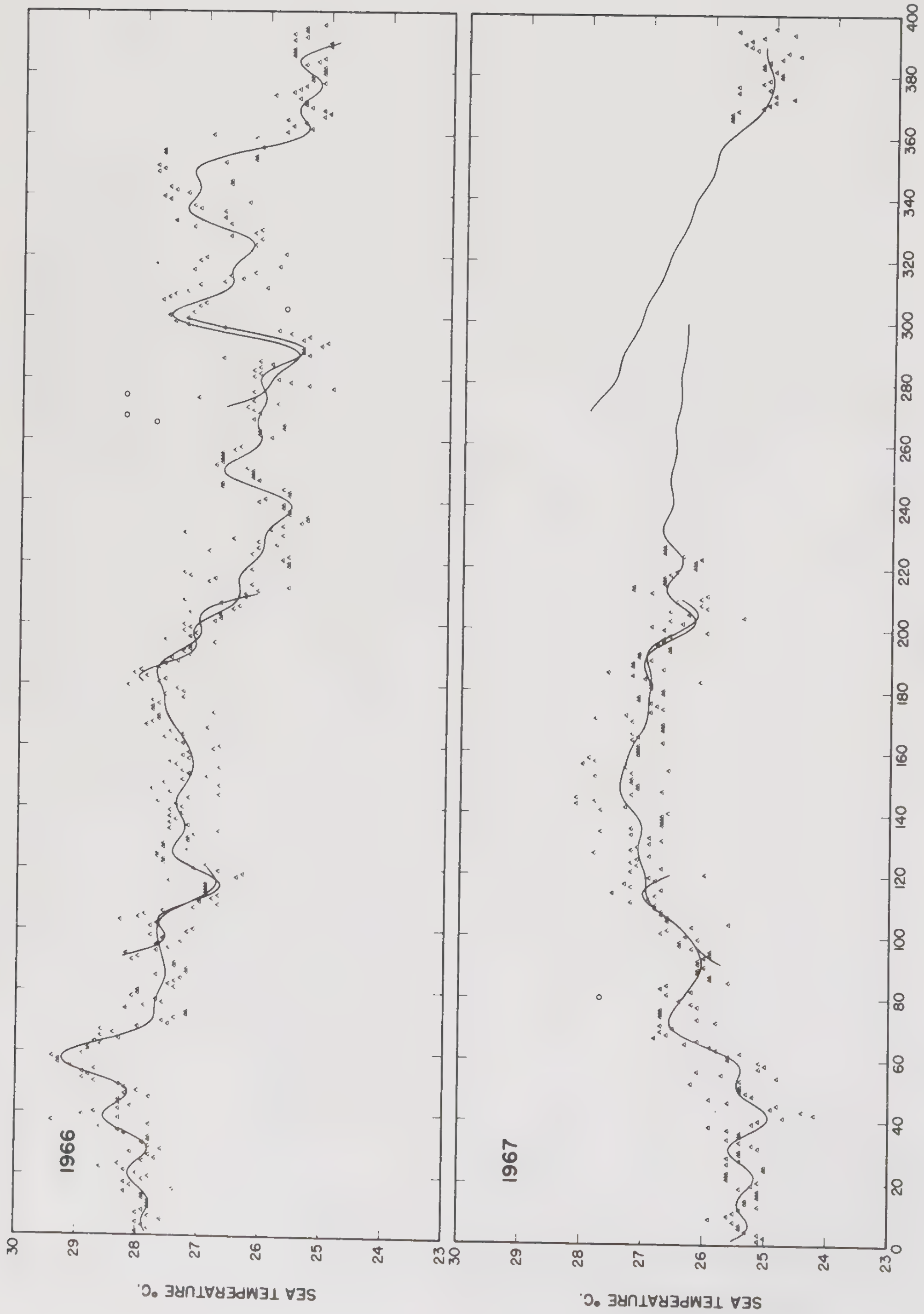
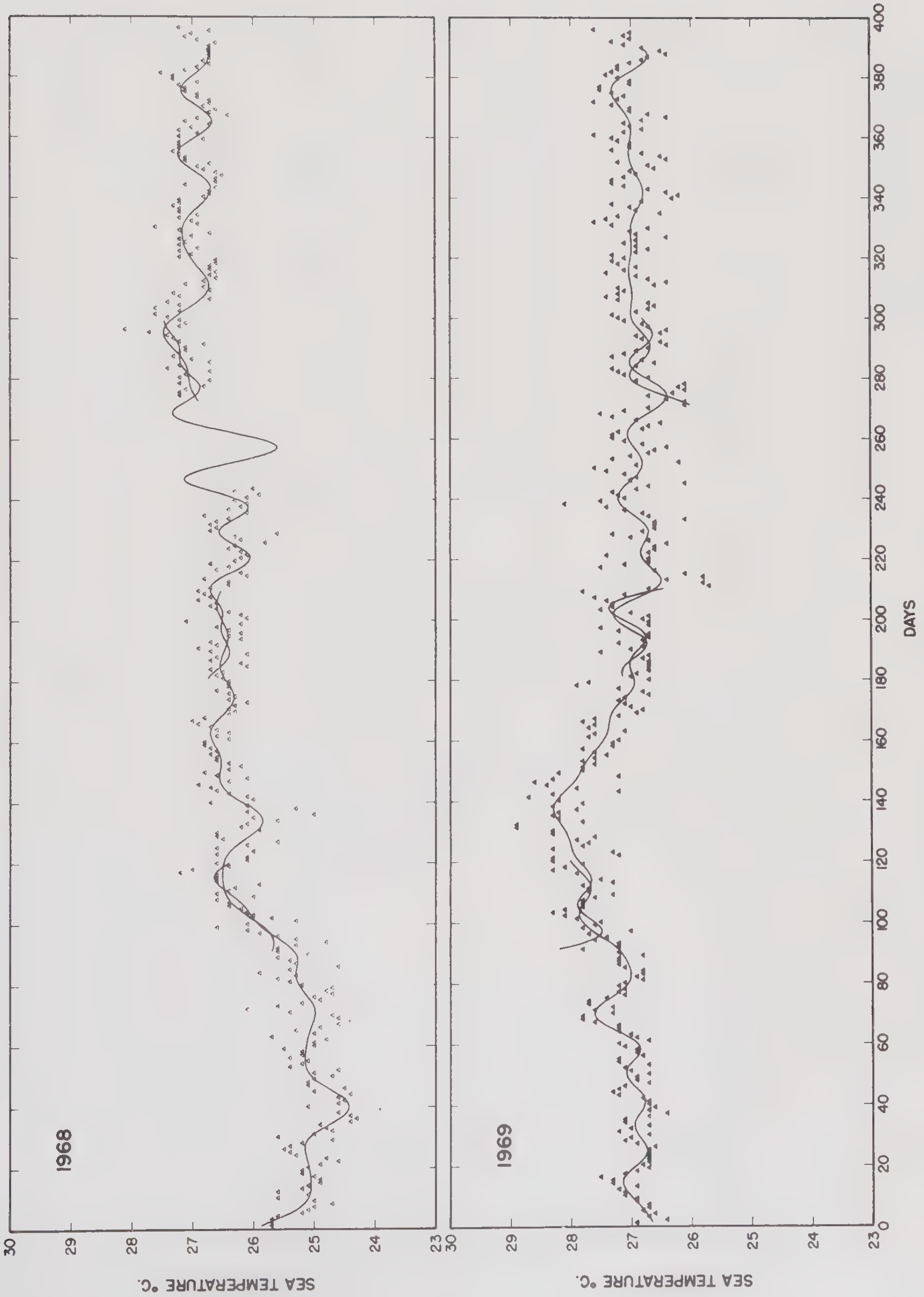


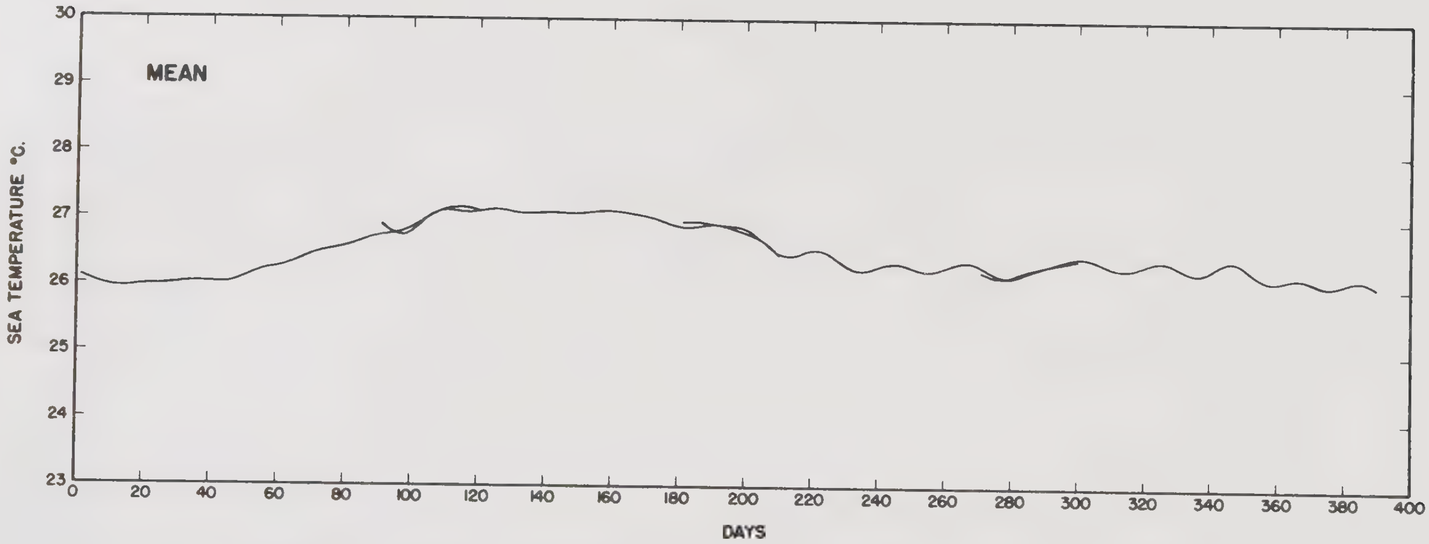
APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*



APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*



APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*



APPENDIX D FIGURE 1.—Sea-surface temperatures, Christmas Island, 1954-69.—*Continued.*

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The Production Of Threadfin Shad As Live Bait For Hawaii's Skipjack Tuna Fishery: An Economic Feasibility Study

by

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July 1971

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FOREWORD

The fishing industry seems to be "natural" for Hawaii. Yet, it accounts for a relatively small percentage of the State's income and employment, and over the last decade or so has failed to keep pace with other sectors of the economy.

The previous study, The Skipjack Tuna Industry in Hawaii: Some Economic Aspects by Dr. Yung Cheng Shang, analyzed the economic problems of the industry. It concluded that the inadequate profit levels were responsible for the current performance of the industry, and that the future of the industry will depend on its ability to increase productivity.

One possible way to accomplish this task is through the development of new bait, an important input to the industry. The current study, sponsored jointly by the Economic Research Center and the National Marine Fisheries Service Hawaii Area Fishery Research Center, evaluates the economic feasibility of producing threadfin shad as live bait for Hawaii's skipjack tuna fisheries. It concludes that such a production would be economically feasible if a yield of 3,660 buckets of shad per 10-acre pond unit can be achieved.

It is hoped that the results of this study will contribute to the solution of the industry's problems and will be useful in directing future research efforts.

Walter Miklius
Director

July 1971
Honolulu, Hawaii

ACKNOWLEDGMENTS

This study was initiated by Mr. Richard S. Shomura, former Acting Area Director, National Marine Fisheries Service Hawaii Area Fishery Research Center.

The authors wish to express their appreciation to Dr. Walter Miklius, Director of the Economic Research Center, Professors Salvatore Comitini and Moheb Ghali of the Economics Department, Dr. John P. Craven, Dean of Marine Programs and Dr. Jack R. Davidson, Director of Sea Grant Program, all of the University of Hawaii, and Dr. Frank J. Hester, Area Director of National Marine Fisheries Service Hawaii Area Fishery Research Center, for reading an earlier draft of this report and offering comments and helpful suggestions.

Appreciation is also extended to Mrs. Mary L. Godfrey of National Marine Fisheries Service Hawaii Area Fishery Research Center for editing the report.

Nonetheless, responsibility for the contents of the study remains with the authors.

Yung C. Shang
Robert T. B. Iverson

July 1971
Honolulu, Hawaii

TABLE OF CONTENTS

Page

ECONOMIC RESEARCH CENTER PUBLICATION POLICY ii

FOREWORD iii

ACKNOWLEDGMENTS iv

TABLE OF CONTENTS v

LIST OF TABLES vi

LIST OF FIGURES vii

LIST OF APPENDIX TABLES viii

I. INTRODUCTION 1

II. AN ESTIMATE OF THE VALUE OF BAIT 3

- The Value of Nehu 3
  - Opportunity Cost 3
  - Total Amount of Bait Required 4
  - Break-even (Maximum) Price of Nehu 5
  - The Results of Calculation 6
- Break-even (Maximum) Price of Shad 10

III. COSTS-REVENUE ANALYSIS OF A SHAD ENTERPRISE 12

- Enumeration of Costs and Revenues 13
  - Initial Costs 13
  - Production Costs 15
  - Salvage Value 15
  - Discount Rate 15
  - Production and Revenue 16
- The Results of Calculation 17
- The Break-even (Minimum) Price of Shad Operation 24

IV. HARVESTING SHAD FROM EXISTING RESERVOIR 31

V. SUMMARY AND CONCLUSIONS 33

APPENDIX 35

LIST OF TABLES

Table		Page
1	Summary of Skipjack Tuna and Bait Catch Records, All Boats Combined, 1965-1969	7
2	Costs of Fishing and Baiting Per Trip	8
3	Estimated Break-even (Maximum) Prices of Nehu by Season . .	9
4	Estimated Break-even (Maximum) Prices of Shad by Season . .	11
5	Construction Costs of Ponds and Bait-holding Facilities .	14
6	Estimated Annual Revenues of Shad Operation by Sources, Levels of Production, and by Mortality Rates	18
7	Net Present Value of Investment in One 10-acre Pond with an Annual Production of 2,440 Buckets of Shad and One 2,000-bucket Bait-holding Facility	20
8	Net Present Value of Investment in One 10-acre Pond with an Annual Production of 3,660 Buckets of Shad and One 2,000-bucket Bait-holding Facility	21
9	Net Present Value of Investment in Thirteen 10-acre Pond Units with an Annual Production of 2,440 Buckets of Shad Per Unit and Six 5,000-bucket Bait-holding Facilities . . .	22
10	Net Present Value of Investment in Nine 10-acre Pond Units with an Annual Production of 3,660 Buckets of Shad Per Unit and Six 5,000-bucket Bait-holding Facilities	23
11	Estimated Break-even (Minimum) Price of Shad Operation for One 10-acre Pond with an Annual Production of 3,660 Buckets of Shad and One 2,000-bucket Bait-holding Facility	29
12	Estimated Break-even (Minimum) Price of Entire Shad Operation (Including Nine Units of 10-acre Ponds and Six Units of 5,000-bucket Bait-holding Facilities) with an Annual Production of 3,660 Buckets of Shad Per Pond Unit	30
13	Net Present Value of Investment in Harvesting Shad from an Existing Reservoir with One Unit of 5,000-bucket Bait-holding Facility	32
14	Estimated Break-even (Minimum) Price of Shad Operation from an Existing Reservoir	32

LIST OF APPENDIX TABLES

Table		Page
A-1	Costs--One 10-acre Pond (Depth: 10 feet)	35
A-2	Costs--Ten 1-acre Ponds (Depth: 10 feet)	36
A-3	Costs--2,000-bucket Threadfin Shad-holding Facility, Fresh Water from a Well	37
A-4	Costs--2,000-bucket Threadfin Shad-holding Facility, Fresh Water Purchased	38
A-5	Costs--5,000-bucket Threadfin Shad-holding Facility, Fresh Water from a Well	39
A-6	Costs--5,000-bucket Threadfin Shad-holding Facility, Fresh Water Purchased	40
A-7	Estimates of the Useful Life of Equipment Associated with Bait-holding Facilities and with Raising Shad in Ponds . .	41
A-8	Costs of Seining Threadfin Shad from Existing Reservoirs .	42

LIST OF FIGURES

Figure		Page
1	The Relationship between the Net Present Value and the Rate of Discount by Levels of Mortality Rate of Shad . . .	25
2	The Relationship between the Net Present Value and the Rate of Discount by Years of Operation	26
3	The Relationship between the Net Present Value and the Rate of Discount by Sources of Fresh Water	27

I. Introduction

The fishery for skipjack tuna, Katsuwonus pelamis, is the most important commercial fishery in Hawaii, producing about 5,000 tons per year. The pole-and-line fishing method used to catch the skipjack requires the use of live bait. A small anchovy called nehu, Stolephorus purpureus, is the major species of bait and constitutes about 92 percent of all baitfish utilized. Nehu are caught by the crew of the tuna boat before leaving for the fishing grounds. The local fleet spends about 30-40 percent of fishing time fishing for bait.[1] This practice limits the number of fishing trips that can be made during the fishing season. In addition, the nehu is a very delicate fish which suffers a substantial mortality rate. The mortality rate averages about 25 percent a day after capture.[2] Fishermen usually fish inshore, generally within 90 miles from the coastline of the main islands, since they must use the bait before mortality becomes heavy.

Attempts have been made to establish a source of baitfish available to the fishermen to minimize the loss of tuna fishing time. The Marquesan sardine, Sardinella marquesensis, has been introduced into island waters; tilapia, Tilapia mossambica, has been cultivated; and artificial bait has also been tried. However, these attempts have not proved successful.

---

[1] Rothschild, Brian J., and Richard N. Uchida. "The Tuna Resources of the Oceanic Regions of the Pacific Ocean," in De Witt Gilbert (ed.), The Future of the Fishing Industry of the United States, pp. 19-51. University of Washington, Publications in Fisheries, New Series, vol. 4, Seattle, Washington, 1968.

[2] Brock, Vernon E., and Richard N. Uchida. Some Operational Aspects of the Hawaiian Live-Bait Fishery for Skipjack Tuna (Katsuwonus pelamis), U.S. Fish and Wildlife Service, Special Scientific Report--Fisheries 574, Washington, D.C., 1968.

Research conducted during the past several years by the National Marine Fisheries Service Hawaii Area Fishery Research Center (NMFS, HAFRC) on the threadfin shad, Dorosoma petenense, has shown this fish to have considerable potential as a substitute live bait for pole-and-line fishing for skipjack tuna.[3] It is hardy, relatively easy to handle, and comparable to the nehu in its tuna-catching ability. In addition, it can be cultured in fresh water impoundments until bait size, and then acclimated to sea water prior to transfer to the fishing boats.

Although this research has established the technical feasibility of using shad as bait, and provides information on input requirements for shad production, the economic feasibility of this production has yet to be determined. In this study we present an evaluation of the economic feasibility of shad production. This evaluation requires a knowledge of the price of the substitute, nehu, in addition to the investment and output data for the shad production.

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[3] Iversen, Robert T. B. Use of Threadfin Shad, Dorosoma Petenense, as Live Bait during Experimental Pole-and-line Fishing for Skipjack Tuna, Katsuwonus pelamis, in Hawaii, U.S. National Marine Fisheries Service Special Scientific Report--Fisheries, No. 641, in press.

II. An Estimate of the Value of Bait

The purpose of this section is to estimate the value of nehu to fishermen, and then to approximate the value of shad by comparing the tuna-catching abilities and mortality rates of nehu and shad.

The Value of Nehu

Due to the vertically integrated nature of the fishing operation in the local skipjack tuna fishery, no market exists for bait. Therefore, an estimate of the value of nehu to fishermen must rely on an indirect approach.

Under certain circumstances, the value of nehu may be estimated by its productivity. This can be done by treating nehu as one of several input factors in the production function of skipjack tuna. The marginal value product of nehu would be its unit value. Due to the limited information available at present, however, a proper production function of skipjack tuna in Hawaii cannot be formulated.

In this study, the value of nehu as a baitfish to local skipjack fishermen is estimated by its opportunity cost approach. The opportunity cost is what fishermen could have earned had they gone fishing instead of baiting. The procedure consists of estimating the income foregone by fishing for bait. This in turn requires estimates of the cost of fishing, the cost of baiting, the demand for bait, and the break-even price for bait.

Opportunity cost. If the fishermen had gone fishing on the days spent baiting, they would have caught an additional quantity of skipjack tuna thereby producing additional income. This additional income would represent the opportunity cost of baiting time to fishermen.

However, the expenses of fishing and baiting are different. A fishing trip requires more fuel and oil than a baiting trip. This difference in expense should be deducted from the opportunity cost. The net opportunity cost should be calculated as follows:

$$C_o = (Q_a \cdot P_t) - (D_b \cdot C_d) \qquad (1)$$

$$= (D_b \cdot \frac{Q_t}{D_f} \cdot \frac{V}{Q_t}) - (D_b \cdot C_d) \qquad \text{assuming fishing rates to be constant}$$

$$= (\frac{D_b}{D_f}) V - (D_b \cdot C_d)$$

where

Q_a = additional poundage of skipjack which could have been caught fishing full time (baiting days eliminated)

P_t = average ex-vessel price of skipjack tuna per pound

D_b = average number of days of day baiting annually

C_d = difference in costs of fishing and baiting

Q_t = average amount of skipjack caught annually

D_f = average number of days of skipjack fishing annually

V = average ex-vessel value of skipjack caught annually

Total amount of bait required. If the fishermen spend full time fishing, they would have to buy the bait instead of catching the bait themselves. In order to catch the additional skipjack tuna, the bait requirements would also have to be increased. It is assumed that this increase in bait requirements would be in proportion to the additional time spent fishing. As mentioned earlier, the mortality rate of nehu is about 25 percent before being used at sea. If the fishermen were to buy the bait required, they would have to pay for the portion which dies. Therefore, the calculation of total bait requirement should be based on the amount of bait caught, or aboard the fishing vessels, rather than the actual amount used, as follows:

$$B_t = B_o + B_a \qquad (2)$$

or

$$B_t = (B_d + B_a)\ (1 + 0.25) \qquad (2\text{-}1)$$

$$B_a = \frac{Q_a}{Q_b} = Q_a \cdot \left(\frac{B_o}{Q_t}\right) \qquad (2\text{-}2)$$

where

B_t = total amount of bait required (buckets, one bucket of nehu is approximately 7 lbs.)

B_o = average amount of bait caught annually (buckets)

B_a = additional amount of bait required to catch additional skipjack (buckets)

B_d = average amount of bait used (buckets)

Q_a = additional skipjack which could have been caught fishing full time (day baiting eliminated)

Q_b = average amount of skipjack caught per bucket of bait

0.25 = mortality rate of nehu

Break-even (maximum) price of nehu. How much would the fishermen be willing to pay for their total bait requirement in order to fish full time? If they paid any amount less than the opportunity cost, they would realize an increase in their total receipts. If the cost of bait were greater than the opportunity cost, the total receipts would be reduced. The break-even price of nehu would be:

$$\frac{C_o}{B_t} \qquad (3)$$

The results of calculation. The intra- and inter-seasonal catch records of skipjack tuna and bait for 1965-1969 for the entire fleet are summarized in Table 1, and the estimated costs of fishing and baiting are shown in Table 2. The difference in costs between fishing and baiting is about $34.5 per trip. The data in Table 1 and 2 were used in equations (1) - (3). The results of the calculation are summarized in Table 3. It is interesting to note that local fishermen are paying about $14 per bucket for bait during the peak fishing months and about $11 during the other fishing months.

In 1953, Brock and Takata[4] used the same concept to approximate the value of nehu. Their finding was that nehu were worth at least $4.23 per pound or about $30 per bucket to the fishermen. When compared with the results of this study it is remarkably high. The 1953 study was based on information for only four boats over a period of one peak fishing month of a good (above average) catching year. In addition, it was based on the amount of bait actually used rather than the amount caught. The difference in costs of fishing and baiting was not considered.

Based on the results of this study, Hawaii's fishermen pay much more than those in Japan and California for their bait. The Japanese tuna fishermen pay about $4.17 per bucket for their live bait. In California live bait is sold for about $1 to $2 per scoop (about 10 lbs).

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[4] Brock, Vernon E., and Michio Takata. Contributions to the Problems of Bait Fish Capture and Mortality Together with Experiments in the Use of Tilapia as Live Bait, Division of Fish and Game, Board of Commissioners of Agriculture and Forestry, Territory of Hawaii, 1955.

TABLE 1

SUMMARY OF SKIPJACK TUNA AND BAIT CATCH RECORDS, ALL BOATS COMBINED, 1965-1969

	Year-round	Peak Fishing Months	Other Fishing Months
	Jan.-Dec.	May-Sept.	Jan.-Apr.; Oct.-Dec.
Total number of fishing trips	10,223	5,946	4,277
Total pounds of skipjack caught (1,000 lbs.)	48,421	35,395	13,026
Total value of skipjack caught ($1,000)	7,384	4,825	2,559
Total number of days of day baiting	4,295	2,428	1,867
Total buckets of bait caught (day and night)	163,844	98,757	65,087

Source: NMFS, HAFRC.

TABLE 2

COSTS OF FISHING AND BAITING PER TRIP

Item	Fishing	Baiting
Hours of operation[a]	14	3 hours day baiting 5 hours traveling
Fuel consumption per hour (gallons)	12.5	5 gallons during baiting 12.5 gallons during traveling
Price of fuel per gallon	\$ 0.20	\$ 0.20
Price of ice	\$15.	--
Total cost[b]	\$50.0[c]	\$15.5[d]

[a] Fishing: 10 hours scouting-fishing and 4 hours traveling time (both ways)

Baiting: 5 hours traveling--about 2 hours to Pearl Harbor, 8 hours to Kaneohe Bay, both ways.

[b] Baiting trip uses less time than fishing trip and allows for more leisure time. The value of leisure time of fishermen is not incorporated in the calculation.

[c] $(14 \times 12.5 \times \$.20) + \$15 = \$50.0$.

[d] $(3 \times 5 \times \$.20) + (5 \times 12.5 \times \$.20) = \$15.5$.

Source: NMFS, HAFRC.

TABLE 3

ESTIMATED BREAK-EVEN (MAXIMUM) PRICES OF NEHU BY SEASON

	Year-round	Peak Fishing Months	Other Fishing Months
Average annual opportunity cost	$588,734	$376,392	$212,342
Total amount (buckets) of nehu required annually	46,513	27,260	19,253
Break-even price of nehu per bucket	$12.7	$13.8	$11.0

Break-even (Maximum) Price of Shad

Once the break-even price of nehu has been determined, the break-even price of shad can be derived by comparing its mortality rate and tuna catching ability with that of nehu. The mortality rate of shad, based on results of preliminary tests, is in the range of 10-16 percent compared with a 25 percent mortality rate of nehu.[5] At sea, the catch rate of skipjack using shad is about equal to nehu, as mentioned earlier. However, due to the lower mortality of shad, the overall catch rate of skipjack per bucket of bait caught is presumed to be about 9-15 percent higher with shad than with nehu. The break-even price of shad is also assumed to be 9-15 percent higher than that of nehu and is calculated as follows:

$$P_s = 1.15\ (P_n) \text{ if the mortality rate of shad is 10 percent} \qquad (4)$$

$$P_s = 1.09\ (P_n) \text{ if the mortality rate of shad is 16 percent} \qquad (5)$$

where

P_s = estimated break-even (maximum) price of shad

P_n = estimated break-even (maximum) price of nehu

The results of the calculations are shown in Table 4. Shad is worth about $15-16 per bucket during the peak fishing months and about $12-13 during the other fishing months.

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[5] Iversen, Robert T. B., and Jay O. Puffinburger. "Capture, Transportation, and Pumping of Threadfin Shad (Dorosoma petenense)," NMFS, HAFRC (manuscript).

TABLE 4

ESTIMATED BREAK-EVEN (MAXIMUM) PRICE OF SHAD BY SEASON

Percent Mortality of Shad	($ per bucket)		
	Year Round	Peak Fishing Months	Other Fishing Months
10	14.6	15.9	12.6
16	13.8	15.0	12.0

III. Costs-Revenue Analysis of a Shad Enterprise

Several measures are available in appraising the economic worth of investments. The two most widely used are the pay-back and the simple rate of return methods. The weakness of both is that they fail to take into account the timing of expected earnings or of expected outlays. In most cases, a large amount of capital must be laid out at the beginning stage of investment, whereas the returns accrue to the investor over a period of time. A dollar in hand today is more valuable than a dollar to be received sometime in the future. Therefore, in this study, the profitability of investment in a shad enterprise is measured by the present value method. This method measures the present value of the associated stream of net receipts, discounted by the appropriate rate of interest, and subtracts the initial costs of the investment. This statement can be expressed mathematically as:

$$NPV = \sum_{i=1}^{n} \frac{(Q_s P_s + I_o)_i}{(1+r)^i} - \left\{ C_o + \sum_{i=1}^{n} \left[\frac{C_i}{(1+r)^i} \right] \right\} + \frac{S}{(1+r)^n} \qquad (6)$$

where

NPV = net present value

Q_s = expected quantity of shad to be produced

P_s = expected price of shad

I_o = other income

C_o = initial construction costs of ponds and bait-holding facilities

C_i = annual production costs

S = salvage value of the assets in year n r = discount rate

i = 1...n (number of years)

If the calculated net present value is positive, investment in a shad interprise would be profitable because the present value of net cash inflow is greater than capital outlay. On the other hand, if the investment has a negative net present value, it would be undesirable from an economic viewpoint.

Enumeration of Costs and Revenues

Initial costs. Initial costs here refer to construction costs of ponds, wells, and bait-holding facilities, as shown in Table 5. The full amount of these costs is treated as initial costs as of time 0. There is no allowance for annual depreciation and no charge for interest.

The construction costs of ponds are estimated on two sizes: (1) one 10-acre pond as one unit and (2) ten 1-acre ponds as one unit. The latter costs more to construct and requires more land area than the former (Appendix Tables A-1 and A-2). Therefore, the second case is not used in the calculations.

The construction costs of bait-holding facilities are estimated on two capacities: 2,000 buckets and 5,000 buckets. For each case, fresh water can be purchased or supplied from a well. The construction cost would be higher for the latter case, while the operation costs would be lower.

The ideal site for fishponds has a ready source of fresh water and is not too far from the harbor. The site for bait-holding facilities

TABLE 5

CONSTRUCTION COSTS OF PONDS AND BAIT-HOLDING FACILITIES

1. Construction Costs of Pond

One 10-acre Pond	10 One-acre Ponds
$63,457	$87,463

2. Construction Costs of Holding Facility

2,000 Buckets Holding Facility		5,000 Buckets Holding Facility	
Water from Well	Water Purchased	Water from Well	Water Purchased
$12,997	$2,456	$14,969	$4,401

Source: Appendix Tables A-1 - A-6.

should be adjacent to the harbor or landing facility where the fishing boats tie up. Land on Oahu is quite expensive to purchase for these purposes. In this study, it is assumed that the land required is leased.

Production costs. Production costs include the costs of operating fishponds and bait-holding facilities, lease rental, as well as the costs of equipment. It varies by the size of fishponds, the capacity of bait-holding facilities and the source of fresh water (Appendix Tables A-1 - A-6). Total cost of equipment varies every year depending upon the physical life of the equipment (Appendix Table A-7).

Salvage value. The normal physical life of ponds and wells is estimated to be about 40 years. However, the loss of value of these facilities due to changes in fishing technology is far less predictable than their physical life. In this study we considered only the physical depreciation. However, shorter physical life periods (20 and 30 years) are used to allow for risk and uncertainty. It is assumed that there is no salvage value after the end of the physical life.

Discount rate. The choice of a proper discount rate is subject to considerable debate. The appropriate rate of discount is the rate of return that might reasonably be expected in an alternate investment. If explicit allowance for risk and uncertainty is made in the estimates of costs and revenue, the rate of return in a riskless investment can be used for discounting. This rate is estimated to be in the 5-7 percent range. If specific allowances for risk and uncertainty are not made in the cost and revenue estimates, an average allowance can be incorporated in the base discount rate. This rate is estimated in the 8-10 percent range. The risk and uncertainty of investment in a bait fishery is assumed to be higher than in other industries because (1) the purse seining technique could be successful for local skipjack tuna fishing in the near future. If this is the case, no live bait may be required; and (2) the population of skipjack tuna may decline in the future after intensive exploitation. Therefore, a 6-14 percent range is used in this study to test the sensitivity of the calculation.

Production and Revenue. Production levels of shad are based on an assumed rate of 200 buckets per 1-acre pond (1 bucket = ca. 5 - 7 lbs.). In a preliminary experiment with no feeding, but with some fertilization, 50 buckets of shad were produced in 1969 in a pond at Makaha, Oahu, Hawaii. The pond had a surface area of 1.4 acres (6,328,000 gal.) when initially stocked and 1.2 acres (3,500,000 gal.) when seined 6 months later. The pond also yielded 420 pounds of tilapia, Tilapia mossambica. With advanced fish culture techniques and a lack of competitors and predators, it may be possible to produce 200 buckets of shad in a 1-acre pond with a depth of 10 feet and containing 2,432,000 gallons of water.[6]

At the present time, it is less likely that 300 buckets of shad can be produced in a 1-acre pond, but with advanced fish culture techniques, it may be possible in the future. Therefore, this high level of production is also included in the calculation.

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[6] This experiment and the levels of threadfin shad production reported by Swingle indicate that further research is necessary to determine if production of 200 buckets per 1-acre pond is attainable. Swingle obtained an average net production of threadfin shad of 122 lbs. per acre over a five-month period in Alabama using two 0.25-acre ponds and two 1-acre ponds. His ponds also produced large amounts of unwanted species, averaging 234 lbs. per acre. (Swingle, Hugh A. Ms., "Production and Growth of the Threadfin Shad, Dorosoma petenense (Gunther), Alone and in Combination with Piscivorous Species," Thesis, Auburn University, Auburn, Alabama, 1967).

The above assumed production levels would result in 2,000 and 3,000 buckets of shad per unit of ten 1-acre ponds. Production levels of 2,440 and 3,660 buckets per one 10-acre pond were extrapolated on the basis of increased volume of water in one 10-acre pond compared to ten 1-acre ponds due to proportinally smaller requirements for levees in the 10-acre pond.

Annual revenue is estimated by multiplying the total amount sold by the price of shad, and adding income from other sources, as shown in Table 6. "Other income" refers to the rental of the tractor-trailer and mobile crane during the months they are not used to haul bait. Total revenue is estimated at two levels of production: 2,440 and 3,660 buckets per unit of 10-acre pond; and by two rates of mortality: 10 and 16 percent.

Shad spawn in the winter and spring in Hawaii and bait-sized fish are available in quantity from May or June through September. Revenues are based on a 4-month period, June through September. There would be no revenues the rest of the year, except those resulting from truck rental. However, it is possible that the fishponds could be used to raise fresh-water shrimp, Macrobrachium rosenbergii, to increase income without affecting the production of shad. Further research is needed, however, before definite statements can be made about this possibility.

The Results of Calculation

The present value calculation of shad operation was done in two ways: (1) on a per unit basis, and (2) the entire operation as one enterprise. Results of the calculation are summarized as follows:

TABLE 6

ESTIMATED ANNUAL REVENUES OF SHAD OPERATION BY SOURCES, LEVELS OF PRODUCTION, AND MORTALITY RATES

A. Value of Shad Production

Levels of Production	Mortality Rate	Break-even Price	Value of Production
2,440 buckets	10%	$15.9	$34,916
	16%	$15.0	$30,744
3,660 buckets	10%	$15.9	$52,375
	16%	$15.0	$46,116

B. Other Income (Rental of tractor-trailer and mobile crane during off season)

$11,480

On a per unit basis: One 10-acre pond with one 2,000-bucket bait holding facility.

The net present values are all negative with the production of 2,440 buckets (Table 7) and are all positive with the production of 3,660 buckets, except when the mortality rate of shad is 16 percent and the discount rate is 14 percent (Table 8).

On the entire operation as one enterprise: Thirteen or nine units of 10-acre ponds and six units of 5,000-bucket holding facilities.

The units required to produce enough bait for the entire fleet during the fishing season are calculated by dividing the total bait requirement by the amount of bait produced per unit, which is one 10-acre pond. To meet the total bait requirement at the peak fishing season (as estimated in Table 3), thirteen or nine 10-acre ponds are required with a unit production of 2,440 or 3,660 buckets, respectively. The number of bait-holding facilities required is derived by dividing the total amount of bait produced by the capacity of a 5,000-bucket holding facility. This is about six units.

The net present values are positive only with a discount rate of 6 percent and with 30 years of operation when the production is 2,440 buckets (Table 9). With the production of shad 3,660 buckets, the net present values are all positive (Table 10).

As expected, the choice of varying discount rates and the mortality rates of shad make a significant difference in calculating the net present value. The higher the rate of discount used, the lower the net present will be; and the lower the mortality rate used, the higher the net present

TABLE 7

NET PRESENT VALUE OF INVESTMENT IN ONE 10-ACRE POND WITH AN ANNUAL PRODUCTION OF 2,440 BUCKETS OF SHAD AND ONE 2,000-BUCKET BAIT-HOLDING FACILITY

		Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
Discount rate	Years of operation	Well water	Water purchased	Well water	Water purchased
Percent		($1,000)	($1,000)	($1,000)	($1,000)
6	20	-54	-52	-105	-103
	30	-47	-46	-105	-104
8	20	-63	-60	-104	-101
	30	-61	-59	-108	-106
10	20	-71	-69	-107	-105
	30	-71	-68	-110	-107
12	20	-77	-72	-109	-104
	30	-71	-67	-105	-101
14	20	-82	-76	-109	-103
	30	-81	-76	-110	-105

TABLE 8

NET PRESENT VALUE OF INVESTMENT IN ONE 10-ACRE POND WITH AN ANNUAL PRODUCTION OF 3,660 BUCKETS OF SHAD AND ONE 2,000-BUCKET BAIT-HOLDING FACILITY [a]

		Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
Discount rate	Years operation	Well water	Water purchased	Well water	Water purchased
Percent		($1,000)	($1,000)	($1,000)	($1,000)
6	20	146	148	75	77
	30	194	195	107	108
8	20	111	114	46	49
	30	136	138	65	67
10	20	78	80	24	26
	30	94	97	35	38
12	20	56	61	6	11
	30	69	73	19	23
14	20	34	40	-8	-2
	30	41	46	-3	2

[a] A 2,000 bucket capacity bait facility would have to be expanded somewhat to process 3,660 buckets of shad but the additional costs are a minor portion of the overall costs.

TABLE 9

NET PRESENT VALUE OF INVESTMENT IN THIRTEEN 10-ACRE POND UNITS WITH AN ANNUAL PRODUCTION OF 2,440 BUCKETS OF SHAD PER UNIT AND SIX 5,000-BUCKET BAIT-HOLDING FACILITIES

Discount rate	Years of operation	Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
		Well water	Water purchased	Well water	Water purchased
Percent		($1,000)	($1,000)	($1,000)	($1,000)
6	20	-19	-85	-641	-707
	30	186	92	-560	-654
8	20	-198	-246	-731	-779
	30	-76	-142	-686	-752
10	20	-338	-371	-800	-833
	30	-265	-309	-776	-820
12	20	-450	-471	-855	-876
	30	-405	-433	-842	-870
14	20	-539	-550	-898	-909
	30	-511	-527	-891	-907

TABLE 10

NET PRESENT VALUE OF INVESTMENT IN NINE 10-ACRE POND UNITS WITH AN ANNUAL PRODUCTION OF 3,660 BUCKETS OF SHAD PER UNIT AND SIX 5,000-BUCKET BAIT-HOLDING FACILITIES

Discount rate	Years of operation	Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
		Well water	Water purchased	Well water	Water purchased
Percent		($1,000)	($1,000)	($1,000)	($1,000)
6	20	1,453	1,383	807	737
	30	1,916	1,818	1,140	1,042
8	20	1,100	1,050	547	497
	30	1,374	1,306	740	672
10	20	826	791	347	312
	30	996	950	465	419
12	20	615	584	187	164
	30	714	684	260	230
14	20	431	418	58	45
	30	498	481	104	87

value (Figure 1). A 30-year operation results in a higher net present value than a 20-year operation. However, this difference is narrowed down when a higher discount rate is used (Figure 2). Fresh water supplied from a well also results in a higher net present value than when water is purchased. But the difference is relatively small (Figure 3). To operate the bait station on a large scale (as one enterprise) is more profitable than on a small scale. The large scale operation needs fewer but larger bait-holding facilities. The construction and operating costs of one large bait-holding facility are less than that of a number of smaller ones.

The Break-even (Minimum) Price of Shad Operation

The break-even price estimated in Table 4 was derived by the opportunity cost approach and it is the maximum price fishermen would be willing to pay for shad. That price was used in the net present value calculation in the previous section.

Now, given the construction costs (ponds and bait-holding facilities), the production costs, the level of production and the discount rate, it is possible to calculate another set of break-even price of shad, which is the minimum price resulting in a zero net present value of shad operation.

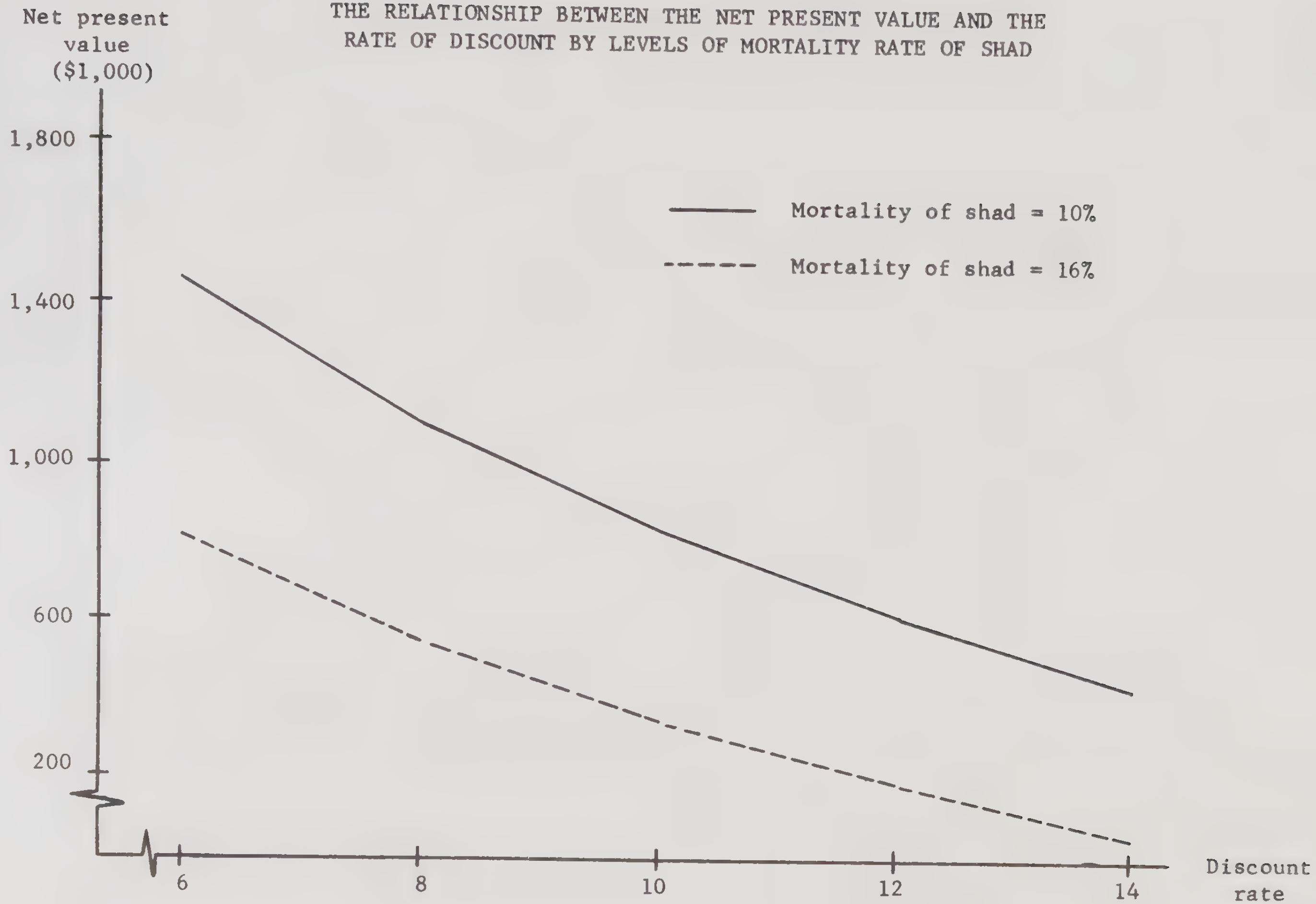
By assuming NPV = 0, then equation (6) can be rewritten as:

$$\sum_{i=1}^{n} \frac{[Q_s \cdot P_s + I_o]_i}{(1 + r)^i} = C_o + \sum_{i=1}^{n} \frac{C_i}{(1 + r)^i} - \frac{S}{(1 + r)^n} \qquad (7)$$

Since the average level of product (Q_s) and other income (I_o) are assumed constant over time, equation (7) can be rewritten as:

FIGURE 1

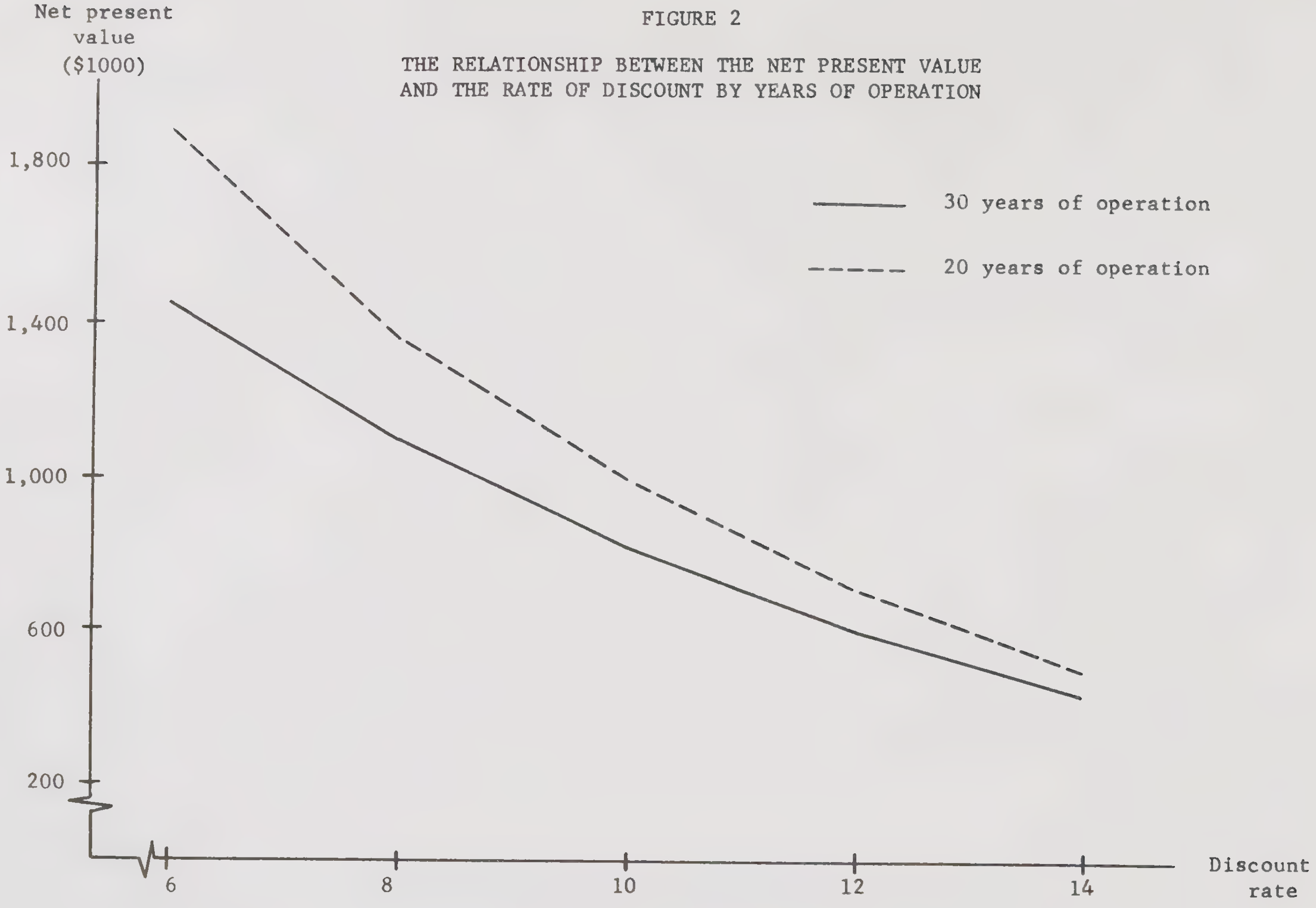
THE RELATIONSHIP BETWEEN THE NET PRESENT VALUE AND THE RATE OF DISCOUNT BY LEVELS OF MORTALITY RATE OF SHAD



Source: Table 10.

FIGURE 2

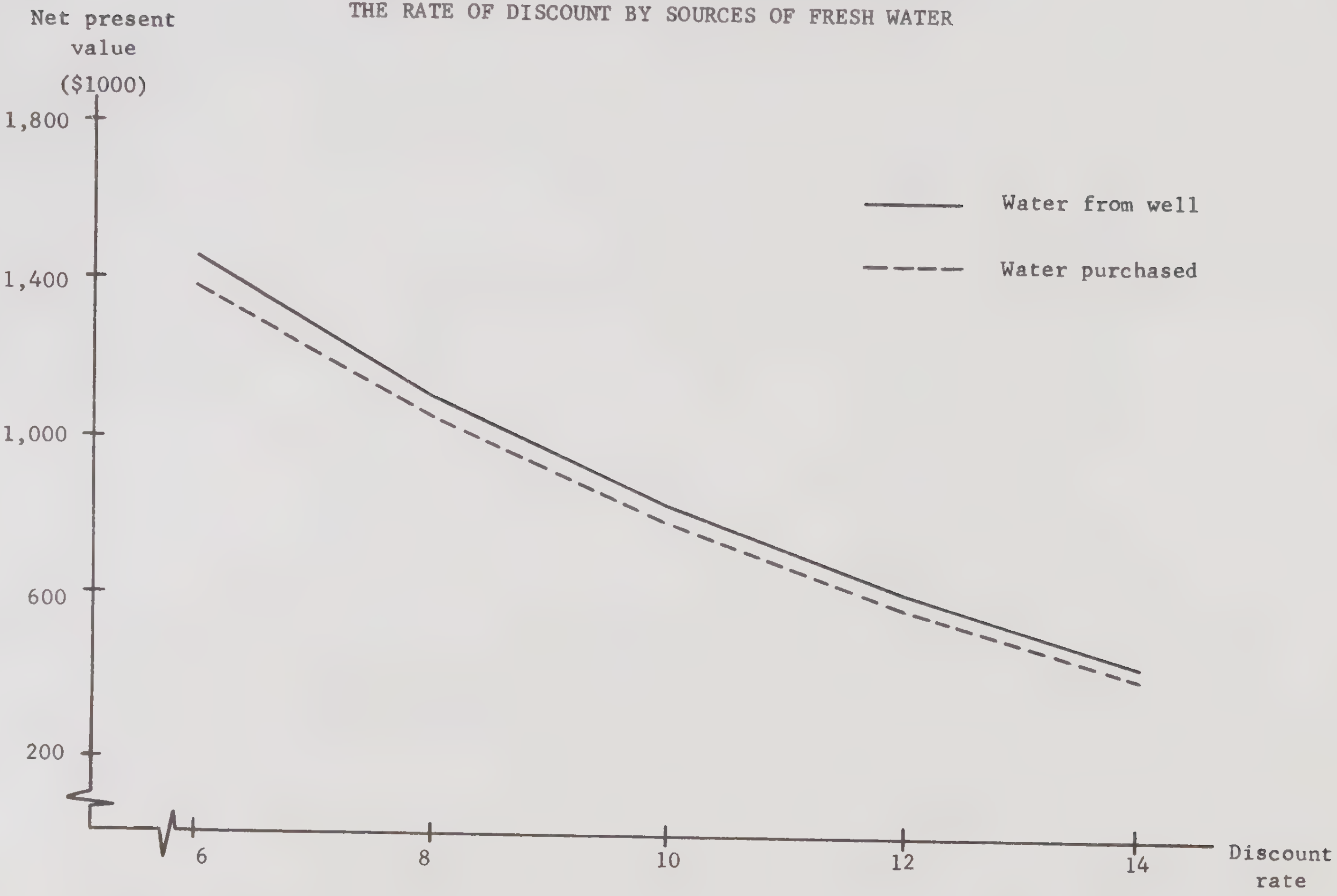
THE RELATIONSHIP BETWEEN THE NET PRESENT VALUE AND THE RATE OF DISCOUNT BY YEARS OF OPERATION



Source: Table 10.

FIGURE 3

THE RELATIONSHIP BETWEEN THE NET PRESENT VALUE AND THE RATE OF DISCOUNT BY SOURCES OF FRESH WATER



Source: Table 10.

$$[(Q_s \cdot P_s) + I_o] \cdot \left[\frac{1 - (1 + r)^n}{r}\right] = C_o + \sum_{i=1}^{n} \frac{C_i}{(1 + r)^i} - \frac{S}{(1 + r)^n}$$

$$Q_s \cdot P_s = \frac{\left[C_o + \sum_{i=1}^{n} \frac{C_i}{(1 + r)^i} - \frac{S}{(1 + r)^n}\right]}{\frac{1 - (1 + r)^n}{r}} - I_o$$

$$P_s = \left[\frac{C_o + \sum_{i=1}^{n} \frac{C_i}{(1 + r)^i} - \frac{S}{(1 + r)^n}}{\frac{1 - (1 + r)^n}{r}} - I_o\right] \frac{1}{Q_s} \qquad (8)$$

The minimum break-even price calculation of shad operation will not be made for those estimates with negative net present values in the previous section. When the net present value is negative, the break-even price of shad operation would be higher than the maximum price the fishermen are willing to pay. This is not feasible from an economic viewpoint. The minimum break-even price is calculated only for those estimates with a positive net present value in the previous section. The results of the calculation are summarized in Tables 11 and 12. The estimated minimum break-even price of shad ranges from about \$11 to \$15 per bucket.

TABLE 11

ESTIMATED BREAK-EVEN (MINIMUM) PRICE OF SHAD OPERATION FOR ONE 10-ACRE POND WITH AN ANNUAL PRODUCTION OF 3,660 BUCKETS OF SHAD, AND ONE 2,000-BUCKET BAIT-HOLDING FACILITY

Discount rate	Years of operation	Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
		Well water	Water purchased	Well water	Water purchased
(%)	(years)	($ per bucket)		($ per bucket)	
6	20	12.0	12.3	12.8	12.8
	30	11.6	11.6	12.5	12.5
8	20	12.6	12.5	13.5	13.4
	30	12.2	12.2	13.1	13.1
10	20	13.1	13.1	14.1	14.0
	30	12.8	12.7	13.7	13.6
12	20	13.7	13.5	14.7	14.5
	30	13.7	13.5	14.6	14.5
14	20	14.3	14.1	15.4	15.1
	30	14.1	13.9	15.1	14.9

TABLE 12

ESTIMATED BREAK-EVEN (MINIMUM) PRICE OF AN ENTIRE SHAD OPERATION (INCLUDING NINE UNITS OF 10-ACRE PONDS AND SIX UNITS OF 5,000 BUCKET BAIT-HOLDING FACILITIES) WITH AN ANNUAL PRODUCTION OF 3,660 BUCKETS OF SHAD PER POND UNIT

Discount rate	Years of operation	Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
		Well water	Water purchased	Well water	Water purchased
(%)	(years)	($ per bucket)		($ per bucket)	
6	20	11.6	11.8	12.5	12.7
	30	11.2	11.4	12.0	12.3
8	20	12.1	12.3	13.0	13.2
	30	11.7	11.9	12.6	12.8
10	20	12.6	12.7	13.5	13.7
	30	12.3	12.5	13.2	13.4
12	20	13.1	13.2	14.1	14.2
	30	12.9	13.0	13.8	14.0
14	20	13.7	13.7	14.7	14.8
	30	13.5	13.5	14.5	14.6

IV. Harvesting Shad from the Existing Reservoir

The Wahiawa Reservoir is in an agricultural region in the interior of Oahu. This reservoir has an area of 302 acres (3 billion gal.) and is used for irrigation and sport fishing. Shad is well established and the reservoir probably contains at least 5,000 buckets of shad in the summer. These shad could be used as a bait supplement assuming there is no conflict with sport fishing in the reservoir.

The economic worth of investment in harvesting shad from the reservoir is evaluated by the same methodology developed in the previous sections. The costs of harvesting shad are summarized in Appendix Table A-8 and the costs of a bait facility (5,000 buckets) are the same as shown in Appendix Tables A-5 and A-6. Since most of the important equipment have to be replaced every 5 or 10 years, the present value calculation is based on a 10-year span.

The results of present value calculations are shown in Table 13. It is noted that all the present values are positive. However, it should be mentioned that the social costs of this operation due to possible conflict with sport fishing are not included in the calculation.

The break-even prices of shad operation from an existing reservoir calculated by using equation (8) are summarized in Table 14. All of them are much less than the maximum price the fishermen are willing to pay.

TABLE 13

NET PRESENT VALUE OF INVESTMENT IN HARVESTING SHAD FROM AN EXISTING RESERVOIR WITH ONE 5,000 BUCKET BAIT-HOLDING FACILITY

Discount rate	Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
	Well water	Water purchased	Well water	Water purchased
Percent	($1,000)	($1,000)	($1,000)	($1,000)
6	108	105	45	42
8	93	92	35	34
10	79	78	27	25
12	68	67	19	18
14	57	57	13	13

TABLE 14

ESTIMATED BREAK-EVEN (MINIMUM) PRICE OF SHAD OPERATION FROM AN EXISTING RESERVOIR

Discount rate	Mortality rate of shad = 10 percent		Mortality rate of shad = 16 percent	
	Well water	Water purchased	Well water	Water purchased
(%)	($ per bucket)		($ per bucket)	
6	10.1	10.2	10.8	10.9
8	10.3	10.3	11.0	11.1
10	10.5	10.5	11.2	11.3
12	10.7	10.7	11.5	11.5
14	10.9	10.9	11.7	11.7

V. Summary and Conclusions

Since no market exists for bait used by the commercial skipjack fishery, the value of bait (nehu) is calculated indirectly by the opportunity cost method. The value of shad is, in turn, derived by comparing the tuna-catching abilities and the mortality rates of nehu and shad.

The economic worth of investment in the shad culture operation is measured by the present value method. The criterion is that if the calculated net present value is positive, investment in a shad enterprise would be profitable. On the other hand, if the investment has a negative net present value, it would be undesirable from an economic viewpoint.

The calculations were made at two levels of production, 2,440 and 3,660 buckets of shad per 10-acre pond unit; two levels of mortality rate of shad, 10 and 16 percent; five levels of discount rate, 6, 8, 10, 12, and 14 percent; two sources of fresh water, from well and to be purchased; two terms of operation, 20 and 30 years; and two ways of operation, on a per unit basis and on the entire operation as one enterprise.

The results of the calculations indicate that the shad operation is feasible with an annual production of 3,660 buckets of shad per 10-acre pond unit and with the selected range of discount rates (6-14 percent). However, it is not feasible with an annual production of 2,440 buckets. The rates of discount and mortality of shad and terms of operation have a significant effect on the profitability of the operation, while the sources of fresh water make no significant difference in profitability of the operation. It can be supplied from a well or purchased. To operate the bait station on a large scale (as one enterprise) is more profitable than on a small scale. The large scale operation needs fewer but larger bait-holding facilities. The construction and operating costs of a large bait-holding facility are less than those of a few smaller ones.

The results of present value calculations also indicate that the investment in harvesting shad from an existing reservoir is profitable if there is no conflict with sport fishing.

Since most of the data used in this study are based on preliminary estimates, future research should be directed in the following areas: (1) study the possibility of raising fresh water shrimp or other species in the ponds to increase income; (2) test the actual mortality rate of shad on commercial fishing boats; (3) determine the maximum production of shad in various sized ponds; and (4) study the feasibility (both technical and economic) of constructing larger size ponds and higher capacity bait facilities to reduce costs.

APPENDIX

Table A-1. Costs--One 10-acre Pond (Depth: 10 feet)

	Cost (dollars)	
COSTS OF CONSTRUCTION:		
Engineering design[a]	8,959	
Excavation and levee construction	41,698	
Well (12" diameter, 150' deep)	10,800	
Access road (500' long, gravel topped)	2,000	
		63,457
COSTS OF EQUIPMENT:[b]		
Pump (800 gpm) and motor (10 hp)	1,442	
Pipes, valves, etc. (8" cast iron, 6" pvc)	839	
Installation of pipes, pump, etc.	448	
Fence (0.67 miles, 4-strand barb wire)	1,000	
Surfacing of levee (grass)	500	
Boat and motor	631	
Harvest equipment		
Fish pump, portable, on trailer	3,600	
Seine	1,770	
Fish transfer hoses	180	
Net handling system (tow-bar)	365	
Pickup truck	2,800	
Water analysis kit	250	
Workshed-storage house	1,000	
Miscellaneous	500	
		15,325
		78,782
ANNUAL OPERATION COSTS:		
Cost of pumping (electricity)	586	
Fish food	2,928	
Fertilizer	244	
Labor	11,550	
Pickup truck, 5,000 miles at .10/mile	500	
Land lease rental (13.5 acres)[c]	2,700	
Maintenance (pond and equipment)	766	
		19,274

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[a] 15 percent of cost of construction and selected equipment.

[b] Total costs of equipment varies every year depending upon the physical life of equipment (Table A-7).

[c] The value of agricultural land ranged from $4,000 to $30,000 an acre. In this study a $10,000 per acre value is used. Land lease rental as a percentage of land value ranged from 2 percent to 6 percent on Oahu. A 2 percent rate is used in this study.

Source: NMFS, HAFRC.

Table A-2. Costs--Ten 1-acre Ponds (Depth: 10 feet)

	Cost (dollars)	
COSTS OF CONSTRUCTION:		
Engineering design[a]	13,053	
Excavation and levee construction	61,610	
Well (12" diameter, 150' deep)	10,800	
Access road (500' long, gravel topped)	2,000	
		87,463
COSTS OF EQUIPMENT:[b]		
Pump (800 gpm) and motor (10 hp)	1,442	
Pipes, valves, etc. (8" cast iron, 6" pvc)	6,552	
Installation of pipes, pump, etc.)	2,016	
Fence (0.7-mi., 4-strand barb wire)	1,100	
Surfacing of levees (grass)	500	
Boat and motor	631	
Harvest equipment		
Fish pump, portable, on trailer	3,600	
Seine	600	
Fish transfer hoses	180	
Net handling system (tow-bar)	365	
Pickup truck	2,800	
Water analysis kit	250	
Workshed-storage house	1,000	
Miscellaneous	500	
		21,536
		108,999
ANNUAL OPERATION COSTS:		
Cost of pumping (electricity)	548	
Fish food	2,400	
Fertilizer	200	
Labor	11,550	
Pickup truck, 5,000 miles at .10/mile	500	
Land lease rental (14.6 acres)[c]	2,920	
Maintenance (ponds and equipment)	783	
		18,901

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[a] See footnote a of Table A-1.

[b] See footnote b of Table A-1.

[c] See footnote c of Table A-1.

Source: NMFS, HAFRC.

Table A-3. Costs--2,000-bucket Threadfin Shad-holding Facility, Fresh Water from a Well

	Cost (dollars)	
COSTS OF CONSTRUCTION:		
Engineering design[a]	2,997	
Site preparation	1,000	
Well (10" diameter, 150' deep)	9,000	
		12,997
COSTS OF EQUIPMENT:[b]		
Pump (200 gpm) and motor (5 hp) for fresh water	1,270	
Pump (300 gpm) and motor (3 hp) for salt water	1,057	
Pipes, valves, etc.	1,831	
Holding tanks (3)	825	
Installation of tanks and water system	1,552	
Fence (chain link)	945	
Salt water filter	1,500	
Bait transfer hose	120	
Pickup truck	2,800	
Mobile crane	12,000	
Tractor-trailer combination (to haul bait)	27,800	
Portable fish tanks (including metal bases)	5,500	
A-frame to lift tanks	200	
Oxygen system	1,050	
Workshed-storage house	1,000	
Miscellaneous	500	
		59,950
		72,947
ANNUAL OPERATION COSTS:		
Labor	9,487	
Cost of pumping (electricity)	289	
Fish food	200	
Oxygen	300	
Vehicles		
Pickup truck 5,000 miles at .10/mile	500	
Tractor-trailer (summer only) 2,000 miles at .30/mile	600	
Mobile crane (summer only)	100	
Land lease rental (7,500 square feet)[c]	1,500	
Maintenance	609	
		13,585

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[a] See footnote a of Table A-1.

[b] See footnote b of Table A-1.

[c] Land value in harbor area is estimated about $10 per square foot. Lease rental is estimated about 2 percent of the land value.

Source: NMFS, HAFRC.

Table A-4. Costs--2,000-bucket Threadfin Shad-holding Facility, Fresh Water Purchased

	Cost (dollars)	
COSTS OF CONSTRUCTION:		
Engineering services [a]	1,456	
Site preparation	1,000	
		2,456
COSTS OF EQUIPMENT: [b]		
Pump (300 gpm) and motor (3 hp) for salt water	1,057	
Pipes, valves, etc.	1,831	
Holding tanks (3)	825	
Installation of tanks and water system	1,552	
Fence (chain link)	945	
Salt water filter	1,500	
Bait transfer hose	120	
Pickup truck	2,800	
Tractor-trailer combination (to haul bait)	27,800	
Mobile crane	12,000	
Portable fish tanks, including metal bases	5,500	
A-frame to lift tanks	200	
Oxygen system	1,050	
Workshed-storage house	1,000	
Miscellaneous	500	
		58,680
		61,136
ANNUAL OPERATION COSTS:		
Fresh water (8.64 million gallons)	1,250	
Labor	9,487	
Cost of pumping (electricity)	155	
Fish food	200	
Oxygen	300	
Vehicles		
Pickup truck, 5,000 miles at .10/mile	500	
Tractor-trailer (summer only) 2,000 miles at .30/mi.	600	
Mobile crane (summer only)	100	
Land lease rental (7,500 square feet) [c]	1,500	
Maintenance	302	
		14,394

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[a] See footnote a of Table A-1.

[b] See footnote b of Table A-1.

[c] See footnote c of Table A-3.

Source: NMFS, HAFRC.

Table A-5. Costs--5,000-bucket Threadfin Shad-holding Facility, Fresh Water from a Well

	Cost (dollars)	
COSTS OF CONSTRUCTION:		
Engineering costs [a]	3,969	
Site preparation	2,000	
Well (10" diameter, 150' deep)	9,000	
		14,969
COSTS OF EQUIPMENT: [b]		
Pump (300 gpm) and motor (10 hp) for fresh water	1,454	
Pump (700 gpm) and motor (10 hp) for salt water	1,369	
Pipes, valves, etc.	3,501	
Holding tanks (7)	1,925	
Installation of tanks and water system	2,768	
Fence (chain link)	1,445	
Salt water filter	2,000	
Bait transfer hose	120	
Pickup truck	2,800	
Mobile crane	12,000	
Tractor-trailer combination (to haul bait)	27,800	
Portable fish tanks (includes bases)	5,500	
A-frame to lift tanks	200	
Oxygen system	1,050	
Workshed-storage	1,000	
Miscellaneous	500	
		65,432
		80,401
ANNUAL OPERATION COSTS:		
Labor	9,487	
Cost of pumping (electricity)	792	
Fish food	450	
Oxygen	750	
Vehicles		
Pickup truck, 6,000 miles at .10/mile	600	
Tractor-trailer (summer only) 4,000 miles at .30/mi.	1,200	
Mobile crane (summer only)	100	
Land lease rental (11,550 square feet) [c]	2,310	
Maintenance	716	
		16,405

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[a] See footnote a of Table A-1.

[b] See footnote b of Table A-1.

[c] See footnote c of Table A-3.

Source: NMFS, HAFRC.

Table A-6. Costs--5,000-bucket Threadfin Shad-holding Facility, Fresh Water Purchased

	Cost (dollars)	
COSTS OF CONSTRUCTION:		
Engineering costs [a]	2,401	
Site preparation	2,000	
		4,401
COSTS OF EQUIPMENT: [b]		
Pump (700 gpm) and motor (10 hp) for salt water	1,369	
Pipes, valves, etc.	3,501	
Holding tanks (7)	1,925	
Installation of tanks and water system	2,768	
Fence (chain link)	1,445	
Salt water filter	2,000	
Bait transfer hose	120	
Pickup truck	2,800	
Mobile crane	12,000	
Tractor-trailer	27,800	
Portable fish tanks (includes bases)	5,500	
A-frame to lift tanks	200	
Oxygen system	1,050	
Workshed-storage house	1,000	
Miscellaneous	500	
		63,978
		68,379
ANNUAL OPERATION COSTS:		
Labor	9,487	
Cost of pumping (electricity)	478	
Fresh water (21.6 million gallons)	2,731	
Fish food	450	
Oxygen	750	
Vehicles		
Pickup truck, 6,000 miles at .10/mile	600	
Tractor-trailer (summer only) 4,000 miles at .30/mile	1,200	
Mobile crane (summer only)	100	
Land lease rental (11,550 square feet) [c]	2,310	
Maintenance	349	
		18,455

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[a] See footnote a of Table A-1.

[b] See footnote b of Table A-1.

[c] See footnote c of Table A-3.

Source: NMFS, HAFRC.

Table A-7. Estimates of the Useful Life of Equipment Associated with Bait-holding Facilities and with Raising Shad in Ponds

Item	Useful life
	Years
Pickup truck	5
Mobile crane	10
Tractor-trailer truck	10
Well	25
Pumps	18
Pipes, valves	30
Earthen ponds	40
Fence (barbwire, around ponds)	5
Fence (chain link, around bait facility)	10
Boat	5
Outboard motor	5
Portable fish pump	10
Seine	3
Transfer hoses	5
Tow-bar system	5
Water analysis kit	5
Workshop-storage house	15
Trailer for skiff	10
Diving gear	5
Bait barge	5
Holding tanks	3
Salt water filter	5
Portable fish tanks	7
A-frame	7
Oxygen system	5
Miscellaneous items	2

Table A-8. Costs of Seining Threadfin Shad from Existing Reservoirs

	Cost (dollars)	
COSTS OF EQUIPMENT:[a]		
Seine skiff	2,000	
Trailer for skiff	1,000	
Bait seine	1,170	
Outboard motor	750	
Fish pump, portable, on trailer	3,600	
Pickup truck	2,800	
Diving equipment	950	
Bait transfer hoses	180	
Miscellaneous (nets, buckets, etc.)	300	
Water analysis kit	250	
Bait barge	1,500	
		14,500
ANNUAL OPERATION COSTS:		
Labor	24,750	
Vehicle, pickup, 4,000 miles at .10/mile	400	
Compressed air for diving	500	
Commercial fishing license	10	
Maintenance	337	
		25,997

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[a] Total costs of equipment vary every year depending upon the physical life of equipment.

Source: NMFS, HAFRC.

7145

H: Indian Ocean

R.S. Shomura

1. TOPOGRAPHY*

The present chapter includes the coastal waters of the Indian Ocean and adjacent seas from Cape Agulhas, South Africa, to the Thailand-Malaysia border (*c.* 6.4°N lat., 100.1°E long.), the southern coasts of Indonesian islands bordering the Indian Ocean, and the west coast of Australia. Also included are the Red Sea, Persian Gulf, and the banks and waters surrounding the islands of the Indian Ocean. (Some of these boundaries, particularly round Ceylon and Australia, which have been used for past statistical tabulation and in this study, are likely to be amended for future statistics.)

The areas of the shelf and slope regions to the 1,000 m depth contour are given in Table H1 adapted from the data of Moiseev (1969).

TABLE H1. AREAS OF SHELF AND UPPER CONTINENTAL SLOPE ON THE INDIAN OCEAN FROM MOISEEV (1969) ('000 KM^2))

Area	*Shelf (0–200 m)*		*Upper Slope (200–1,000 m)*	
East Africa	390		440	
South Africa (east of 30°E)		140		100
Mozambique		120		180
Tanzania-Kenya		10		160
Somalia		120		
Arabian Sea	400		300	
Arabia and Gulf of Aden		80		140
India–Pakistan West Coast		320		160
Bay of Bengal	610		240	
India–Pakistan East Coast		190		140
Burma		250		40
Thailand-Malaysia		170		60
Indonesia	130		100	
Western Australia	380		90	
South Australian Coast (to 130°E)	260		90	
Red Sea	180		200	
Persian Gulf	240		—	
Madagascar	210		100	
Oceanic Islands	(200)		(100)	
Total	3,000		1,600	

Brackets denote approximation.

Except for the relatively wide shelf zones in the eastern sector of the Arabian Sea, the eastern sector of the Bay of Bengal and the northwest coast of Australia, the continental shelf of much of the Indian Ocean and adjacent seas is extremely narrow and in places precipitous. Along the East African coast, the 200 m contour line is in many places less than 4 km from shore. In addition to the narrow shelf, coral reefs and coral outcroppings are found throughout the area, especially along the African coast.

The Red Sea extends in a general northwest–southeast direction for about 2,200 km and has a maximum width of 352 km in the vicinity of Massawa in the south. The average depth of the Red Sea is about 700 m, with some deep pockets exceeding 2,000 m. The northern sector has some shallow areas which are trawlable, e.g. in the Gulf of Suez, but for the most part the northern waters are considered to be too deep for trawling. The continental shelf widens in the central and southern Red Sea and in some areas in the south sector the shelf extends for more than 100 km offshore.

The Persian Gulf is a relatively small body of water covering approximately 239,000 km^2 with an average depth of 35 m and a maximum depth of 150 m. An indication of the extent of shallow areas is indicated in the northern sector, off Iraq, where the depth is only 8 fm at 46 km offshore.

2. HYDROGRAPHY

2.1 Currents

The striking feature of the surface currents in the Indian Ocean is the reversal occurring in the northern parts—Arabian Sea and Bay of Bengal—following the changes in the wind system with the monsoons. This has no close parallel in other oceans.

The current system in the southern Indian Ocean is similar to those in the Atlantic and Pacific. The South Equatorial Current flows westward at around 10°S, dividing as it approaches the African coast. The southward flowing arm branches each side of Madagascar, uniting to form the Agulhas Current. The West Wind Drift, and a weak and rather confused northward flowing current off Western Australia, completes the anticlockwise gyre in the southern Indian Ocean.

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* The boundary between Eastern and Western Indian Ocean around Ceylon has been changed for the purposes of future statistics.

In the northern Indian Ocean, during the southwest monsoon (April–September) the Somali Current flows northwards along the coast of Africa as a swift and narrow current; speeds as high as 7 knots have been reported (Swallow 1965). The width of the Somali Current at the Equator has been estimated at 9 km and the current widens to about 74 km farther north. At the height of development, the Somali Current reaches as far north as 12°N lat.; however, most of the water leaves the coast and flows in an easterly direction as the Monsoon Current south of 10°N lat.

In the Gulf of Aden, the flow of the surface current is from the Gulf into the Arabian Sea from June through August. Along South Arabia, the currents are weak and move in an east and northeasterly direction; along India, the flow is in general southerly.

In the Bay of Bengal, the flow pattern during the southwest monsoon period is generally northeast. Upon reaching the continental coast, most of this water turns southward and flows along the continental shelf. South of Sumatra, the current flows southeasterly along the coast of Sumatra and merges with southeast Asian water flowing into the Indian Ocean through the Timor Sea. These waters form the basis of the South Equatorial Current in the Indian Ocean. It should be noted that during some months there is a southerly flow of water along the east coast of India.

The northeast monsoon (October–March) brings about considerable changes in the circulatory pattern, especially in the northern seas. The Somali Current reverses direction and flows southerly from December through February. Surface current flow in the Gulf of Aden is from the Arabian Sea into the Gulf. For much of the northern sector of the Arabian Sea, the surface currents are weak and variable with no one direction generally prevailing. For a brief period, November–December, a weak current flows northward along the coast of India. In the Bay of Bengal, a cyclonic circulation occupies the entire Bay in February; however, this pattern does not prevail during the entire northeast monsoon period.

2.2 Upwelling

Zones of upwelling have been discovered in various localities throughout the area under consideration. In the Arabian Sea, one of the most pronounced zones of upwelling occurs in waters off South Arabia from Kuria Muria Bay to Ras al Haad during the southwest monsoon. The upwelling appears to be seasonal; there is no evidence that upwelling occurs during the northeast monsoon.

In the Arabian Sea, a second pronounced area of upwelling occurs off northern Somalia within 40 km of the coast (Swallow 1965). Although the cold water is rich in nutrients, there is very little evidence of a high level of biological activity. A high standing crop of plankton is evident only in the northern part of the cold water area, in the vicinity of Cape Guardafui.

In the Bay of Bengal, La Fond (1958) reported areas of upwelling along the east coast of India during the southwest monsoon. Wyrtki (1961) indicated that some upwelling seems to develop in the Andaman Sea during the northeast monsoon.

Possibly the most important upwelling occurs in the eastern Indian Ocean south of Java. Wyrtki (1962) estimated the extent of the area of upwelling as 400 km wide and 1,200 km long. He computed the rate of flow of water as 2.4 million m^3/sec.

Another area of upwelling in the eastern Indian Ocean occurs off the northwest coast of Australia. Rochford (1962) showed that in the area of upwelling the inorganic phosphate values in the surface waters measured 0.3 μg at/l, values considerably higher than the 0.1 μg at/l for adjacent waters.

A general review of the upwelling areas of the world, and their biological productivity has been given by Cushing (FAO, 1969).

In addition to the areas listed by Cushing, there appears to be an important upwelling area off southwest India (Banse 1968).

3. PRIMARY PRODUCTION

Except for some areas along the west coast of India, eastern south Africa (Burchall 1968), and the west coast of Australia, very little published information is available on primary production of coastal waters in the Indian Ocean. Undoubtedly, efforts during the International Indian Ocean Expedition (IIOE) have added considerable amounts of biological and oceanographic data to the fund of information of the Indian Ocean; however, data on phytoplankton and zooplankton are still inadequate for proper evaluation of the total annual standing crop still less of production, in time and space.

Ryther and Menzel (1965) provided some indication of the richness of the waters off South Arabia. On two stations occupied off the Gulf of Oman, they obtained values of 5.7 and 6.4 gC/m^2/day, values which compare favourably with waters off Peru. As shown in the Atlas of the Arabian Sea for Fishery Oceanography (Wooster *et al.* 1967), data on primary production in the Arabian Sea are sparse and inadequate to provide anything but a general indication of the production of the northern Arabian Sea. For the June–July–August period data, only five C^{14} observations were available to Wooster *et al.* (1967). Undoubtedly, more measurements have since been made; to date these data have not been made available. It is doubtful, however, that all of the observations made to date add to a large total.

Subrahmanyan (1959) provides the only estimate of the phytoplankton production for the entire west coast of India. He considered an area 1,200 mi (2,000 km) long (coastline of west India) by 50 mi (90 km) wide and estimated the production to be 1.813 million tons, wet weight.

4. ZOOPLANKTON

Much of the zooplankton data collected during IIOE are still being processed and analyzed. It is doubtful, however, that these data are sufficient to give more than a generalized view of the zooplankton distribution in coastal waters of the Indian Ocean. Tranter (1962) estimated the average standing crop of zooplankton from the Australian continental shelf waters as 100 mg/m^3 and less than 50 mg/m^3 for the open ocean. He further indicated that the waters of the upwelling area off northwest Australia were as rich as waters over the continental shelf.

The standing crop in the Indian Ocean was included in the world summary given by Bogorov *et al.* (1968). These studies show few rich areas in the Indian Ocean. A density of 200 mg/m^3, found in most of the fertile areas of the North Atlantic and North Pacific, and a large part of the upwelling areas off the western Americas and west Africa, is reached in the Indian Ocean only on a narrow band along the western Indian peninsula, and off southern Arabia. The general level in the coastal as is 100–200 mg/m^3.

5. FISH STOCK AND FISHERIES

The marine catch from the Indian Ocean and adjacent seas is about 2 million metric tons (see Appendix Table H6). On the basis of yield per unit surface area, the Indian Ocean yield was only about 1/5 of the Atlantic and the Pacific yields (FAO, 1967a). Much of this relatively low yield can be attributed to the low level of fishing effort, using for the most part primitive gear of the type employed in subsistence fishing. Fishing in many parts of the coastal waters of the Indian Ocean, especially along Africa, is still carried out in non-motorized boats with simple gear. Large-scale fishing with large vessels is confined to (1) the high seas long-lining for tunas and billfishes conducted by fishermen of Japan, USSR, China (Taiwan) and more recently Korea, and (2) bottom trawling and purse seining, in the Gulf of Aden and waters off south Arabia, by USSR, southern European and Japanese fishing vessels, though this has been effectively halted since the closure of the Suez Canal in 1967.

5.1 The fisheries

(a) East African Coastal Region (South Africa, Mozambique, Tanzania, Kenya)

Much of the fishing carried out along the east African coastline is of a subsistence type and confined to the immediate coastal waters. Presently, the fish species exploited include *Sardinella*, seerfishes, sharks, and various demersal and pelagic fishes which are caught throughout the area. Recent attempts to catch sardines and other small schooling pelagic fish with purse-seines and stick-held dipnets (bouke-ami) using light in Tanzania waters have met with fair success. Catches in the purse-seine fishery have averaged 1.8 tons/boat/night during the period 1963–6.

Very little experimental bottom trawling has been conducted in this area. For the most part, the results have been negative and indicate that trawl gear cannot increase the fish yield in east African waters. The lack of success has been attributed to the extensive coral outcroppings in this area and to the narrowness of the continental shelf. Trawling, however, should not be ruled out, since most of the trawling was done by large vessels working in shallow depths. It is possible that successful results could be achieved with small trawlers. A similar situation existed in the Gulf of Thailand, where only after the introduction of offshore trawling with small boats and small nets did the fishery flourish (Tiews 1966).

(b) Arabian Sea

Very little fishing is carried out in western Arabian Sea, more because of the lack of markets for a local fishery than through lack of fish. A rough estimate of 100,000 tons has been made for the catch of sardinella in Muscat and Oman, caught close along the shore. Recently a number of long range trawlers from Greece, USSR and Japan have worked off the southern coast of Arabia and northeast coast of Somalia, reporting catches of some 30 tons/day; the number of those ships has decreased since the Suez Canal was closed.

Important shrimp fisheries, discussed in detail in another chapter, have developed in waters off Iran and off Kuwait, Qatar, and other Arabian States and along the Pakistan and Indian west coast.

The Indian west coast also supports important traditional fisheries, particularly the seasonal fishery for sardinella and mackerel. This fishery, and the other fisheries for shrimp and bottom fish, are all carried out by medium to small vessels with a limited radius of action.

(c) Bay of Bengal

In the northern parts of the Bay of Bengal the fishing season begins in November and ends in February, principally because of the rough weather brought on by the southwest monsoon. The fishing gear consists primarily of drift nets, set nets, stake nets, and longlines. Trawling for demersal fish is conducted throughout the area. The most important fishery in East Pakistan is for the threadfin (*Polynemus indicus*).

The fishery resources along the Indian Ocean coast of Thailand were until recently virtually untapped. Marketing problems, primarily resulting from the long distances from population centres, and the emphasis on trawling in the Gulf of Thailand have until recently retarded the development of the west coast fisheries.

The Thai fishery in this area has expanded very rapidly since 1966, many fishing boats being transferred from the east coast, and newer and larger boats (20–25 m) have been built. 1967 catches of mackerel (*Rastrelliger*) by Thailand were around 45,000 tons. The longer established Malay fishery in the Strait of Malacca is at present at around the same level.

(d) Indonesia

The estimated catches for the southern coasts of the Indonesian islands bordering the Indian Ocean are provided in Appendix Table H6. The catch for Indonesia was obtained by taking 25% of the total Indonesian marine catch. The basis for this separation is that the available literature, which is extremely limited, indicates that most of the fishing takes place in the northern waters. The important species include sardines, anchovies (*Stolephorus* spp.), mackerel, mackerel scad, and skipjack tuna. One of the most important fisheries for sardine occurs in the strait between east Java and Bali. All the fishing is carried out by small boats, usually close to shore and with simple equipment.

(e) Western Australia

The catches of fish (in the narrow sense) round western Australia are very small. Some catches of Australian salmon (*Arripis trutta*) are taken inshore along the southwest coast, and local fishermen take a variety of other species in small quantities. Japanese trawlers have worked occasionally off the northwest coast. The large fisheries are for crustaceans, which are discussed in the relevant chapter. The stocks of crayfish (spiny lobster, *Panulirus cygnus*) seem fully exploited in the present areas, but offer potential for expansion from Shark Bay and Exmouth Gulf northwards. The shrimp fishery has been expanding steadily northwards to Shark Bay and Exmouth Gulf.

(f) Red Sea

Presently the major fisheries in the Red Sea are the sardine fisheries in the northern part of the Red Sea, and along the Ethiopian coastline, and the bottom trawl fishery in the southern waters of the Red Sea. Ben Tuvia (MS), who provides the most comprehensive review of the fisheries in the Red Sea, indicated that the northern waters did not appear to be productive enough to support much more than is being taken at present. To date, efforts to harvest tunas in commercial quantities with purse-seine, longline, and gillnets have met with little success (Ben-Yami 1964). Also, the purse-seine and light method used successfully to catch sardines and other small pelagic fishes in other areas has not been very successful in the Red Sea.

(g) Islands and banks

With some exceptions, e.g. the trawl fishery of Ceylon and a small tuna fishery operating from Minicoy Islands in the Maldive Island Chain, most of the island fisheries have been of the subsistence type using predominantly handlines, set nets, and traps, catching a variety of species, mainly bottom living species. In Madagascar, a shrimp fishery for export has recently developed.

5.2 Statistics

Basic catch and effort statistics are virtually non-existent for much of the Indian Ocean. In many areas, some subsistence fishing undoubtedly goes unreported, thereby under-estimating the reported total catches. In other areas, e.g. Burma, the reported catch has not changed over the years, a condition highly improbable and one which indicates a lack of adequate data.

The fisheries of western Australia, especially the crustacean fisheries, have probably the best statistics; fair statistics are also available for the fisheries of India. Long-range fishing, except for tuna, is still very uncommon, so that information on place of landing also gives good information on place of capture.

5.3 Stock assessments

(a) Demersal fish

The Wadge Bank off southern tip of India, with an area of 4,000 n.mi^2 (13,500 km^2) is one of the few areas where even approximate assessments can be made. It has been fished for many years by trawlers from Ceylon, and there exist good records of these operations, which have been going on, with interruptions, for some 50 years (Mendis 1967). It has also been fished by Indian vessels from Tamil Nadu and Kerala coasts, but statistics of these catches are not available.

Until 1966, only two or three trawlers operated, but recently five new stern trawlers have been added to the fleet. The total catch in 1967 was 2,000 tons, compared with peak production in early years of under 1,500 tons. (These figures exclude quantities of low valued fish rejected at sea, estimated by Mendis as some 20%).

Sivalingam (1966, MS) has studied the relation between the amount of fishing and the catch per unit effort, considering separately three groups of species; the larger resident species (snappers, etc.), smaller resident species, and migrants (mainly carangids), the last being only caught in quantity during the southwest monsoon. For the big fish, he noted a decline in both catch per unit effort and average size when fishing was increasing, and deduced that the maximum sustained yield of these species was around 500 tons. The catch per unit effort of smaller species showed no decline, probably because of a shorter life-span, less intense fishing, and a possible switch in fishing attention onto these as the larger species declined. Though in the period studied the smaller species never totalled more than half the larger species, it is probable that their potential is as large. The heavily exploited area is only a fraction of the total bank —estimated by Sivalingam (MS) as 1,250 n.mi^2 out of the total of 4,000 n.mi^2. The density of the unexploited areas is presumably less, but even if it is only half that of the exploited areas the total potential in the former areas would be slightly greater. Altogether, making some allowance for migration between exploited and unexploited areas, the total annual potential of the two first groups of species on the whole bank may be rather more than five times the potential of big fish in the exploited parts, say 2,500–3,500 tons.

The most recent information of the species composition of the trawl catch has been given by Fernando (1970); 66% were resident species, the rest being migrants, appearing only in the southwest monsoon, nearly equally divided between carangids, elasmobranchs, and catfish (*Netuma thalassinus*). Since the migrants appear in the catches for half the year only, it is a reasonable supposition that the ratio of potential to present catch is twice that for resident species. This implies a total potential of 5–7,000 tons.

Two independent estimates of the fish stocks have been made. Mendis (1965) estimated the total standing stock, from trawl catches, and the area swept by the trawl, as 18.5 million lb, or 8,500 tons. Using the formula, potential = 0.5 × unfished standing stock × natural mortality, this would be consistent with the above estimate if natural mortality were 1.2–1.6; these seem rather high, but Mendis' data referred to a period of moderately heavy exploitation, when the standing stock would be less than in the unfished condition. The two estimates are, therefore, in fair agreement.

Mendis (1967) also obtained estimates, based on the primary production, of the potential fish production of 54 million lb (25,000 tons) of all species of fish, 65% of which would be good quality. This estimate is very sensitive to the precise figure used for the efficiency of transfer from one trophic level to another, as well as to the position of the fish in the food chain. It, therefore, agrees moderately well with other estimates, but suggests that the upper figure (7,000 tons) is perhaps the more likely. This implies a potential of bottom fish of about 5 kg/ha.

A rough assessment can also be made for the area off Karachi. Zupanovic (FAO internal reports) has noted that locally fishing appears very intense, and the local stocks are probably fully exploited. This applies only to depths out to about 15 fm (30 m) and to the area close to Karachi, i.e. to a strip about 20–25 n.mi wide, and perhaps 80–100 n.mi long, with an area of *c.* 7,000 km^2. Landings of demersal fish at Karachi averaged around 20,000 tons in 1965–7, presumably mostly from the heavily fished area, equivalent to a yield of a little under 30 kg/ha. Assuming that this could be increased somewhat by better management, the potential might be as much as 40 kg/ha.

Exploratory fishing: Ocean islands and banks

A quantitative survey of the ocean banks, e.g. by trawling, is made difficult by the rough ground. Wheeler (1953) lost three trawls without catching a fish, and based his estimates of standing stock on line fishing. His technique was to allow the ship to drift sideways, thus effectively sweeping an area equal to the length of the drift times the width, taken as 40 ft, the distance apart of the outside lines. Clearly this could easily result in over-estimates if fish are attracted in from outside the path (especially likely for sharks), or an under-estimate if not all the fish in the path take the bait. In particular, the smaller fish will be greatly under-estimated. However, the data do provide a first estimate of the standing stock.

These estimates, derived from the data of Wheeler (1953, section VI) are given in Table H2. The totals differ from his totals of 1.1 million tons of fish, and 0.8 million tons of sharks because there appears to be an arithmetical mistake in his estimate for the Sava de Malha corpus. Making allowance for the other banks and islands, e.g. the Maldives, not included in Wheeler's study, suggests a total standing crop of about 0.5 million tons of larger bottom fish and sharks.

For sharks, the above figures are more likely to be an over-estimate than an under-estimate of standing crop; also, due to the low fecundity and long life of sharks the potential yield is probably a small fraction of the unexploited standing stock. Probably the potential yield on the banks is no more than around 100,000 tons, unless there is continual immigration from the open oceans.

For the other fish (*Lutianus* spp., *Lethrinus* spp., etc.), the standing stock is less likely to be over-estimated, and the potential is likely to be a bigger fraction of it. Little is known of the average life-span of these fishes. There is some general experience with reef fisheries that initially high catch rates cannot be maintained, which suggests a

TABLE H2. ESTIMATES OF STANDING CROP OF LARGE FISHES AND SHARKS AROUND THE ISLANDS AND BANKS OF THE WESTERN INDIAN OCEAN (DERIVED FROM WHEELER 1953)

	Fishable area	*Tons/mi^2*		*Total standing crop (tons)*	
	(n.mi^2)	*Fish*	*Sharks*	*Fish*	*Sharks*
Chagos					
Speakers Bank	216	39.4	48.3	8,510	10,432
Peros Banhos	117	31.2	4.5	3,650	526
Great Chagos	2,000	41.3	65.3	82,600	130,600
Pitt Bank	100	5.6	53.1	560	3,310
Total	2,433			95,320	144,868
Oceanic Banks					
Hawkins Bank	70	1*	30*	70	2,100
Soudan Bank	240	8.5	5	2,040	1,200
Nazareth Bank, south	900	8.5	6.9	7,650	6,210
Nazareth Bank	3,100	22.3	7.5	69,130	23,250
Sava de Malha, coccyx	100	2.1	62	210	6,210
Sava de Malha, corpus	4,450	26.9	18.3	119,705	81,435
Sava de Malha, cervix	700	48.4	65	33,880	45,500
Sava de Malha, caput	150	26	67.3	3,900	10,095
Fortune Bank	126	5.2	84.3	655	10,622
Constant Bank	200	8.8	41.5	1,760	8,300
Anivantes	640	26.6	23.7	17,024	15,168
Total	10,676			256,024	210,090
Seychelles	3,000	15.5	18.7	46,500	56,100
Total (n.mi^2)	16,109	24.7	25.5	397,844	411,058
Total (km^2)	55,300	7.2	7.4		

* Estimated from catch per man.

low rate of replacement, and presumably also of mortality. However, the natural mortality in tropical waters, even of relatively long-lived fish, may be higher than is common in temperate waters, so that the potential may be half to a quarter of the unexploited standing crop. Allowing for some under-estimation of this latter, the potential of the larger bottom fish may be around half the estimated standing crop, in Table H2, i.e. 0.25 million tons (the figures of 9.8 and 2.8 million tons given by Wheeler appear to be due to a confusion between total quantity and quantity per mi^2, on the Soudan Bank). This is equivalent to about 12 tons per mi^2 or 3.5 tons per km^2. This is about a little greater than the existing yields estimated by Wheeler for the waters around Mauritius (10 tons/mi^2), which were believed to be over-exploited.

No estimate is possible of the potential of the smaller reef fishes, not vulnerable to the type of line fishing used by Wheeler.

Coastal trawling

In the western Indian Ocean (off the Arabian and African coasts) little exploratory fishery has been done. Some experimental trawling has been done by Kenya and by the East African Marine Fisheries Research Organization. Catches of teleosts have been light, and this may be attributable to the clear water, and the fact that most of the demersal fish live near the coral, where trawls cannot be used.

In the northern and eastern part of the area—in the arc from West Pakistan around India to Malaysia—there has been during the last decade a large amount of exploratory and research trawling, much of which, and also a summary of earlier surveys, was reported to the 1968 IPFC Symposium on Demersal Resources (Rao 1970). These operations were carried out by a variety of different vessels, using a wide range of gears, and operating in different ways—on a semi-commercial basis, with fishing concentrated on the best areas, or on a predetermined grid, etc. Too much, therefore, should not be made of these data in the way of detailed comparison between areas, though they can be used to provide a rough guide to the potential, particularly the species composition, and the depth distribution.

Exploratory fishing off West Pakistan has been described by Hussain *et al.* (1970); these operations, by M.F.V. *Machhera* (52 tons, 120 hp engine) were restricted to waters within 70 mi. In some areas, e.g. off Karachi, catch rates have been falling during the period of the surveys (1960–7), and this decrease appears to be due to the heavy fishing there. The average catch per hour was 44 kg—or 0.37 kg/HP/hour. Of this a proportion 10–30% was inedible or unmarketable fish which were discarded at sea.

Further exploratory fishing in the offshore waters of West Pakistan (outside 12 mi, down to 1,000 m) was carried out in the early part of 1969 by USSR vessels, in collaboration with Pakistan. In the western part, to the Ras Malan Cape the narrow shelf and steep continental shelf offered no suitable trawling grounds. In the other part, off Karachi and the mouth of the Indus, some good catches were taken. Between 25 m and about 100 m catches by the vessels (RTM and SRTM type) were around 1.0–1.5 tons/hour or about 0.2–0.3 kg/HP/hour. Beyond 100 m catches tended to decrease, becoming small at 300 m, and the limited number of hauls between 800 m and 1,000 m caught virtually nothing.

The results of the exploratory fishing by Government of India vessels between 23°10′N and 15°N has been summarized by Rao *et al.* (1970). The larger vessels (*c.* 300 bhp, 120 GRT) averaged 194–387 kg/hour in different latitudinal zones, the lowest being at 18°N, south of Bombay, and catches increasing to the north and south, being approximately equal at 22°N (365 kg/hour) and 15°N (387 kg/hour). Some, at least, of the differences may be due to the heavier fishing around Bombay.

In terms of depth, best catches were between 50 and 60 m (365 kg/hour), decreasing to around 100 kg/hour both in deeper water (80–90 m)—though few hauls were made at this depth—and in shallow water (<10 m)—though the smaller vessels may have made relatively more hauls on these depths. There appeared to be a tendency for the optimum depth to increase from south to north.

Slightly different variations of catch rates with depth for catches by commercial bull-trawlers from Bombay were noted by Rao (1969). Most fishing (*c.* 78%) was done between 25 and 45 m, with catches around 900 kg/hour. About the same weight per hour was caught in shallow water, but were less valuable species—nearly half of those in the 16–20 m zone were elasmobranchs. Catches in deeper water decreased to only 420 kg/hour in 71–75 m, the deepest zone fished.

The seasonal range in catch rates was relatively small, perhaps surprisingly so in view of the big environmental changes due to the monsoon; the best month was August (310 kg/hour) and the worst January (166 kg/hour).

Trawling in the south-western region (from Cape Cormorin to 15°N) has been described by Rao (1967, 1969). The area includes some rich shrimp grounds, discussed separately, but fish catches were rather poor, around 100 kg/hour, but higher in the north (off Mangalore) mainly of small sized uneconomic varieties. Towards the end of 1967 the surveys were extended into deep water off Cochin where good catches of deep sea prawns (*Parapandalus*, *Aristacus*, etc.) were taken (Rao 1970), but it is not known how large the fish catches were.

Catches off the east coast of India have been discussed by Rao (1969). Catch rates tended to increase from south to north, and were generally lower than on the Indian west coast. Government of India vessels from the Tuticorin base operating between Cape Cormorin and Pondicherry (12°) averaged 106 kg/hour in 1961–5, those from the Visakhapatnam base (mainly fishing between 17°N and 21°N), averaged 120 kg/hour. Rather higher rates (210 kg/hour) were achieved by Indo-Norwegian Project vessels fishing in the Gulf of Nannar and Palk Bay, but nearly all the catch (over 90%) were low valued silver bellies (Leiognathidae).

Surveys in the northern part of the Bay of Bengal have been carried out in collaboration between FAO and West Pakistan (FAO 1965, internal reports of the UNDP(SF) project). The best fishing (up to 500 kg/hour) is in a band about 20 km wide between 5 and 30 fm (10–60 m), extending from off the Indian border to

Coxes Bazar. Catches in water deeper than 60 m were very poor.

Observations off southern Burma have been reported by Druzhinin and Hlaing (1970). Catches of F.V. *Linzin* (250 tons, 500 hp) averaged around 200 kg/hour, being rather higher in the southern (around 13°N), than in the northern (*c.* 14°N) part of the survey area.

Finally exploratory fishing has recently been carried out by Thailand off her west coast; catches have been comparable with those in the Gulf of Thailand in the period before the development of large-scale trawling.

Most of these areas are only lightly fished for demersal species, except very close inshore. The exception is off the west coast of India and Pakistan, especially near Bombay and Karachi, where fishing is intense; despite this, catch rates in the area are good. Fishing is also heavy around Cochin, mainly for shrimps, and the catches of fish are poor. It appears, therefore, that the parts of the Indian Ocean Shelf area covered by these surveys can be roughly grouped into three classes:

Rich: Exploited—fair catch rates (over 200 kg/hour), India–Pakistan west coast, from Karachi to *c.* 15°N
Fair: Little exploited—fair catch rates; or exploited—poor catch rates, Indian west coast, south of 15°N; northern and eastern coasts, Bay of Bengal
Poor: Little exploited—poor catch rates (150 kg/hour, or less), Indian east coast

To convert these qualitative descriptions into quantitative estimates, the only data from the area are the estimates above—5 kg/ha on the Wadge Bank, and 40 kg/ha off Karachi. The basic productivity off Karachi is higher than on the Wadge Bank, but the difference is not so great as the 1:8 ratio in fish potential. It may be that the lower figure does not take full account of the smaller and less valuable species not sought out by the trawlers.

Two other figures for the Indo-Pacific region have been obtained in the section on the Western Central Pacific—25 kg/ha in the Yellow Sea, and 50 kg/ha in the northern part of the Gulf of Thailand. Putting these together suggests potential annual yields per unit area of 50 kg/ha in the rich zone, 25 kg/ha in the intermediate zone, and 10 kg/ha in the poor zone, though these figures should be considered only as rough approximations, with a range of perhaps ± 50%.

These estimates, again in default of anything better, may be extrapolated to other parts of the Indian Ocean. To the westward, it appears likely, from the oceanographical conditions, that the richness of the grounds off the northwest Indian peninsula is continued round the coast of the Arabian Sea, including the east coast of Somalia, probably as far as 5°N. The rest of the coast of east Africa south to the Zambesi appears to be unproductive; in any case, the shelf is narrow, so that the total bottom resources are small and the steepness and roughness of the bottom makes bottom fishing, at least with nets, difficult. Further south, the potential may be rather higher. In default of further evidence the density of stocks round Madagascar will be assumed to be similar to that off the African coast.

These very rough estimates for the bottom resources of the western Indian Ocean may be summarized as in Table H3.

A similar extrapolation can be made to the southeastward. The area off Malaya is probably similar to that off Thailand, i.e. with a moderate production.

Little is known of conditions along the western coasts of Indonesia, but there is at least local upwelling, and productivity may be high.

Japanese trawlers have worked off northwest Australia, but not very intensely or for a long period, so that the potential is probably no more than average.

The potential of the eastern part of the Great Australian Bight was considered in the chapter on the Southwest Pacific. It appears to be a very poor area, with a potential estimated from exploratory fishing, at only 0.5–3 kg/ha. Probably the southern Australian coast, west of 130°E, has a similar potential of say 2 kg/ha.

The potential bottom fish catches for the eastern Indian Ocean can be summarized as in Table H4—with the reservation that the estimates are in all cases very tentative.

TABLE H3. POTENTIAL DEMERSAL RESOURCES OF THE SHELF REGIONS OF THE WESTERN INDIAN OCEAN

Region	*Area* *('000 km^2)*	*Density* *(kg/ha/year)*	*Potential* *('000 tons/year)*
South Africa	140	25	350
Mozambique	120	25	300
Tanzania–Kenya	10	10–20	10–20
Somalia (2°S–5°N)	50	10–20	50–100
Somalia (north of 5°N)	70	50	350
Arabia and Gulf of Aden	80	50	400
India–Pakistan (north of 15°N)	245	50	1,250
India (south of 15°N)	75	25	180
Red Sea	180	10	180
Gulf of Iran, Iraq, Kuwait etc.	240	25	600
Madagascar	210	25	525
Total	1,420		4,225
Oceanic Islands (larger fish only)			250
Total, all bottom fish			4,475, say 4,500

TABLE H4. POTENTIAL BOTTOM FISH RESOURCES OF THE SHELF AREAS OF THE EASTERN INDIAN OCEAN

Region	*Area* (*'000 km²*)	*Density* (*kg/ha/year*)	*Potential* (*'000 tons*)
India–Ceylon (south of 20°N)	85	10	80
India–Pakistan (north of 20°N)	105	25	260
Burma	250	25	625
Thailand–Malaysia	170	25	425
Indonesia	130	50	650
Western Australia	380	25	950
Southern Australia	260	2	50
Total	1,380		3,040, say 3,000

(b) Pelagic fish

There seems little doubt that the small shoaling pelagic fish (sardine, anchovies, mackerels, etc.) form a large resource in several parts of the Indian Ocean, especially in the Arabian Sea, and one that is less than fully exploited (e.g. Panikkar and Dwivedi 1966). There is, however, very little information from which this general impression of rich resources can be expressed in a quantitative form.

The biggest present catches of pelagic fish are taken off the Indian southwest coast. The most important species is the oil sardine (*Sardinella longiceps*) of which the catches fluctuated widely. The worst recent year was 1956 (7,400 tons) and the best 1964 (274,000 tons) (Prabhu 1967); in the last few years catches do not seem to have fluctuated so much (Appendix Table H7). The reasons for the fluctuations are not known with complete certainty. Possible reasons are real changes in the abundance of the stocks (year-class changes), or changes in the pattern of migration (nearly all fishing is done close inshore, and if the fish remain offshore catches would be low). Bennett (1968) suggests the fluctuations are of year-class strength, correlated with the abundance of the existing stock.

There is no evidence that fishing is having any serious effect on the stock; equally, the natural fluctuations are such that fishing could be having a large effect without being detectible, especially since the same pattern of fishing—large numbers of small inshore vessels—has been in existence for some time without much change. Also there are no good records of total fishing effort.

The same remarks hold good of the other major pelagic fishery round India, that for Indian mackerel (*Rastrelliger kanagurta*). Fishing takes place on both coasts, and recent catches have fluctuated between 25,000 (1964) and 130,000 tons (1960) (Venkatavaman 1967).

Substantial and increasing catches of mackerel (*R. kanagurta* and *R. neglectus*) are being taken by Thailand and Malaysia on the eastern side of the Bay of Bengal, and in the Strait of Malacca; it is believed (Menasveta personal communication) that the Thai and Malaysian fishermen, each taking 40–45,000 tons of fish in 1967, are harvesting the same stocks of mackerel. Stock assessment studies carried out by Thai scientists suggest that this stock is being exploited at about the optimum level, and little increase of total catch can be achieved. The Thai fishery on the Indian Ocean coast has developed very recently, and though results of stock assessment studies are not yet available, it is likely the effects of this new fishery will soon become apparent, and enable some quantitative estimate of the resources to be made.

In the other fisheries in which substantial quantities of pelagic fish are probably caught along the coast of the Arabian peninsula, and off Indonesia, reliable information even of total catch is not available, still less any data from which assessments could be made.

Eggs and larvae

Wide-spread collection of fish eggs and larvae were made during the International Indian Ocean Expedition (IIOE), but have not yet been fully worked up and published. An analysis of the numbers of eggs and larvae, without distinction of species, has been made by Peter (1967). The maximum concentration of eggs (over 400/haul) occurred east of Socotra Island, and in the Gulf of Oman. Larvae were common in these areas, and also off the central part of the Indian west coast, and at the head of the Bay of Bengal. A preliminary examination has been made of the species composition of samples from 50 stations by Ahlstrom (1968). These were grouped into three zones—oceanic (19 stations), intermediate (27 stations) and coastal (4 stations).

The oceanic stations were dominated by larvae of deep sea fishes, two families (Myctophidae and Gonostomatidae) accounting for three-quarters of the larvae caught.

The intermediate stations also contained large numbers of these families, but in addition numbers of anchovies (12% of the total) and of several predominantly demersal families (*c.* 20% in all) were caught.

In the very limited number of coastal stations anchovies again accounted for about 13% of the total, and nearly all the other identifiable larvae belonged to bottom-living groups (Scorpaenidae, etc.).

A surprising feature of the collection, noted by Ahlstrom, was that only one clupeoid larvae was found, and no specimens of *Rastrelliger*, though a few *Rastrelliger* larvae had previously been identified by Peter (1967) in other IIOE material.

The data are too few to attempt quantitative assessments, but some general conclusions seem valid.

(a) As in other regions, myctophids and gonostomatids form a major resource in the oceanic areas.

(b) There is a large resource of engraulids (anchovies).
(c) The oil sardine and mackerel resources are not extremely large, and their potential may not be much above present catch levels.
(d) In the coastal zone the demersal species may form the bulk of the potential fish resource.

The distribution of both eggs and larvae, without separation by species or family, has also been shown in charts issued after the Indian Ocean Expedition (Anon 1970), covering the whole Indian Ocean. The larval distribution shows high abundance in the north-western area (from Mombasa around to Muscat), and also off southern India. More surprising features are the high abundance (over 100 larvae per haul) in the western Bay of Bengal, and the relatively low abundance (less than 25 per haul) southwest of Indonesia.

Another approach to the estimation of resources is from primary production.

On the basis of some measurements of primary productivity in the Arabian Sea area, Schaefer (as reported in FAO. 1967) indicated that the potential yield from the Arabian Sea could be as high as 10 million metric tons. The study made by Subrahmanyan (1959) is interesting in that it represents another estimate of the potential yield from a relatively large portion of the coastal waters of the Arabian Sea. On the basis of his studies on phytoplankton, Subrahmanyan estimated the phytoplankton production along the 1,200 mi (2,224 km) coast of India and extending offshore for 50 mi (93 km) as 1.8 × 109 metric tons. Subrahmanyan indicated that the annual catch of fish from the west coast of India for the period 1950–4 was about 455,000 tons; the fish catch was thus computed to be 0.025% of the phytoplankton production. He compared this ratio with that for the English Channel, an area of intensive fishing. For the English Channel, Subrahmanyan stated that the 1928 fish catch was 71,000 tons and the phytoplankton production was estimated at 15 million tons. If the assumption is made that the fish-phytoplankton relationship of 0.06% for the English Channel is a reasonable average figure, then the fish yield from the west coast of India could be increased by a factor of 2.5 to 1.119 million tons. This is approximately equal to the estimated demersal potential of the area given in Table H3.

Cushing (FAO, 1969) in his review of the upwelling areas of the world estimated that the carbon fixation in the upwelling areas of the western Indian Ocean was 70×10^6 tons, with a corresponding estimate of production at the tertiary level of around 10×10^6 tons wet weight. He also gave corresponding estimates for the area of northwest Australia and Java, of 50×10^6 tons carbon, and $7–8 \times 10^6$ tons wet weight of tertiary production. He believed that half to one-third of the production could be harvested by man, giving estimates of say 4 million tons in the Arabian Sea, and 3 million tons in the Java–Australian zone. Probably, in common with other upwelling areas, most of the production is of pelagic fish. This is in general agreement with the demersal estimates in Tables H3 and H4 of 0.65 and 1.6 million tons respectively; these would imply other potential resources of about 3.5 and 1.5 million tons, most of which are likely to be shoaling pelagic fish. These estimates are probably as reliable as can be obtained with present information.

Off the Indian west coast, the egg and larval data, and the close agreement between estimated demersal potential and potential estimated from primary production suggest that the pelagic potential is not very great. A guess might be a little higher than recent catches, say 500,000 tons, though this could be an under-estimate.

In the Bay of Bengal, and eastward to Malaysia, there is very little evidence concerning the pelagic potential. In the northern part, off East Pakistan, vessels of the FAO/UNDP project have noted echo traces in mid-water, which might be small fish or zooplankton; though extensive they are rather diffuse and do not suggest a very promising resource. Also the traces do not extend far offshore over the deeper water. Probably in this area the pelagic resources of shoaling fish (sardines, mackerel, etc.) are rather less than those of demersal fish, and may be of the order of 1 million tons, for the whole Bay of Bengal.

In the extreme southeast of the Indian Ocean, south of the Indonesia-northwest Australian upwelling area, there is again very little information on pelagic fish. The estimate of demersal potential, principally derived from limited exploratory fishing on the Great Australian Bight is very low—50,000 tons. The pelagic potential may not be much higher—say of the order of 100–200,000 tons.

The western side, off the African coast south of the Somalia upwelling area, does not appear to be highly productive. The nature of the coast generally with a steep and narrow concentrated shelf suggests that the pelagic resources are likely to be rather larger than the demersal ones—estimated in Table H3 as 730,000 tons. One million tons is a round figure which might be a fairly reasonable estimate.

Mass mortalities

A feature of the northwest Indian Ocean has been the occasional occurrence of dead fish on the surface over wide areas. The most striking such mass mortality occurred in 1957 when quantities estimated as high as a million tons occurred in the central Arabian Sea between 60° and 70°E, and 10° and 20°N (Pannikar and Dwivedi 1966). The species concerned have not been definitely identified, but the occurrence confirmed the existence of large fish resources of some kind in the area.

A more local mortality has been reported by Foxton (1965), who found large numbers of small inshore species (mostly porcupine fish, *Cyclicthys echinatus*) close inshore between 9° and 12° along the Somali coast, probably killed by the upwelling of cold water. The quantity of fish observed was probably consistent with the estimates of potential noted above.

Cephalopods

There is little information about the resources of cephalopods in the area, even in comparison with the same data on fish. Almost certainly the production of larger animals in the upwelling areas will include a substantial quantity of squids, possibly at least several hundreds of thousands of tons.

6. SUMMARY AND DISCUSSIONS

The estimates in the above sections may be summarized in round figures as shown in Table H5 (including also estimates of crustacean and tuna resources taken from the relevant chapters).

These figures should be treated with a fair degree of caution; the tuna and larger crustaceans are likely to be fairly accurate, the others, with the exception of the cephalopods, are probably accurate within a factor of two, and possibly within 50% of the true value. They do show with a fair certainty that present total catches of fish from the Indian Ocean could be greatly increased, even if some individual stocks (large tuna, some shrimp, possibly some local stocks of demersal fish) are fully exploited.

TABLE H5. ESTIMATED POTENTIAL ANNUAL CATCHES ('000 TONS), FROM THE INDIAN OCEAN

Species	*Western Indian Ocean*	*Eastern Indian Ocean*
Demersal fish	4,500	3,000
Shoaling pelagic fish	4,000	2,000
Tunas and skipjack	–300–	
Crustaceans	150	100
Cephalopods	(×100)	(×100)

Much can be done to improve the estimates. Assessments of existing fisheries could be improved by better statistics of catch and fishing effort, plus related data on size and (where possible age) composition, growth, mortality rates and stock separation. While there is a large volume of biological data on fish in the Indian Ocean, little of it is directly related to the commercial fisheries.

Though most of the observations made on the IIOE are not immediately useful for estimating resources, some of the data could be so used. In particular, the examination of collections of material of eggs and larvae could be carried forward from the preliminary analysis described above to provide a much better estimate of the adult stock and spawning distribution of the major species. Such examination may show whether further egg and larvae surveys, in selected times and areas, might produce useful information at reasonable cost.

Other surveys which appear likely to yield useful results are trawl surveys in the less known areas, especially in deeper water off most coasts, and along the Indonesian coasts. For pelagic fish, echo surveys seem especially promising. Promising traces have been observed by oceanographic vessels off southern Arabia, but a systematic survey, preferably backed up with a fishing vessel with suitable equipment (purse-seine, or mid-water trawl) should provide much better estimates of the magnitude of the resource, and of the practical prospects of developing a fishery. Other fruitful areas for such surveys appear to be off the Indian west coast, especially beyond the range of the existing fishery (this may well reveal whether or not most of the stocks are being exploited) and off Indonesia.

TABLE H6. CATCHES FROM THE INDIAN OCEAN ('000 METRIC TONS)

Country	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
South Africa (a)	3	3	3	3	3	3	3	3	3	
Mozambique	3	3	4	4	4	5	5	6	7	
Madagascar	4	4	5	6	8	18	17	17	18	
Tanzania	16	17	19	20	22	29	29	13	12	
Kenya	5	5	5	5	6	7	6	6	7	
Somalia	4	4	4	...	...	...	...	...	...	
Ethiopia	17	14	9	12	15	13	11	...	...	
UAR	...	25	24	18	15	12	...	...	...	
Saudi Arabia	16	18	20	20	19	20	22	25	30	
Southern Yemen	47	54	55	52	52	50	40	46	...	
Muscat, Oman (a)	100	100	100	100	100	100	100	100	100	
Iran	...	...	...	...	...	19	19	...	...	
Pakistan (West)	67	73	76	88	98	131	129	130	150	
India (West coast)	521	487	492	677	654	680	664	700	708	
Maldives	...	...	12	12	20	22	25	24	32	
Ceylon	71	79	88	96	87	97	106	135	...	
India (East coast)	163	157	164	184	171	210	200	204	204	
Pakistan (East)	36	35	42	46	44	44	51	52	58	
Burma	360	360	360	360	360	360	381	396	414	432
Thailand	23	27	32	22	16	30	114	162	...	
Indonesia	105	109	112	118	133	144	136	188	197	
Australia	...	...	...	44	46	56	59	66	55	
Japan	5	127	100	81	91	87	131	126	105	
China (Taiwan)	8	8	9	9	7	4	14	37	38	
Korea	—	—	—	—	—	1	4	12	19	
USSR	—	...	2	5	36	76	38	10	21	
Total (b)	1,530	1,660	1,680	1,960	1,980	2,170	2,260	2,420	2,700	

Notes: (a) Estimates
(b) Includes catches by countries not listed separately
... No data
— Information zero

TABLE H7. CATCHES OF MAJOR SPECIES AND SPECIES GROUPS FROM THE INDIAN OCEAN ('000 METRIC TONS)

Species/Species group	1962	1963	1964	1965	1966	1967	1968	1969
Salmonids	1	6	7	6	6	3	3	8
Shads, etc.	15	15	17	18	19	16	13	13
Flatfish	18	10	7	11	9	8	12	15
Gadoids	3	7	5	7	5	4	3	3
Basses, croakers, etc.	257	257	266	270	337	321	316	346
Bombay Duck (India)	84	92	81	74	77	75	82	76
Jacks, mullets, etc.	...	...	86	77	93	100	87	73
Sardines, anchovies	271	215	431	416	430	407	462	353
Oil sardine (India)	110	64	274	262	253	259	301	174
Oil sardine (Pakistan)	5	6	7	8	9	10	10	12
Tunas	...	...	155	168	179	234	276	231
Mackerels	...	...	30	47	35	75	86	135
Rastrelliger (India)	29	77	24	43	32	29	21	92
Rastrelliger (Thailand)	...	...	6	4	3	46	65	43
Elasmobranchs	80	86	82	83	97	95	99	118
Unsorted and unidentified fish	616	638	661	677	730	763	815	977
Crustaceans	120	121	160	134	156	168	176	202
Shrimps (India)	83	82	95	77	91	92	100	108
Shrimps (Pakistan)	14	14	21	22	22	25	23	26
Molluscs	...	...	11	15	18	25	35	21

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7146

I: Western Central Pacific

R.S. Shomura

1. TOPOGRAPHY

As defined here the northern boundary runs from the southern tip of Korea to 130°E, 20°S, thence eastward. The western and southern boundaries are the mainland coast of Asia and the Malay Peninsula to 100°E long., thence south to Sumatra, and along the Sumatra–Java–Sunda island chain to 130°E long., the northern coast of Australia to the Torres Strait, the coast of New Guinea, and east to 180° long. (A revised northern boundary running to the south of Taiwan is being used in future FAO statistical tabulations.)

The region includes wide areas of continental shelf. From the north these are given in Table I1 (with approximate areas in km^2, and n.mi^2 (in brackets) to the 200 m contour):

TABLE I1. AREAS OF SHALLOW WATER IN THE WESTERN CENTRAL PACIFIC (UNDER 200 M)

Area	*n.mi*^{2}	*km*^{2}
Yellow Sea and East China Sea (to the north end of Taiwan)	(275,000)	950,000
Formosa Strait and Chinese south coast	(82,000)	280,000
Gulf of Tongking (to 15°N)	(58,000)	200,000
Gulf of Thailand (from Cape Cambodia to Malaysia–Thailand border)	(89,000)	305,000
South China Sea (from 15°N to the Equator)	(280,000)	970,000
Java Sea (from the Equator south and east to Bali)	(170,000)	580,000
Gulf of Carpentaria and the eastern Arafura Sea	(280,000)	960,000
There are also narrower areas of continental shelf and shallow waters round the oceanic islands; the approximate areas are:		
Southwest coast of Japan	(16,000)	50,000
Ryukyu Islands	(3,000)	10,000
Philippines	(63,000)	215,000
Eastern New Guinea, Solomon Islands, etc. (north of 10°N)	(27,000)	90,000

Note: Those areas are only approximate, particularly for the areas surrounding islands with narrow shelves. They have been estimated from the charts in Philip's Mercantile Marine Atlas (14th edition, 1952) which gives the 100 fm contour. There does not seem to be detailed presentation of the size of the shelf in the region. Menard and Smith (1966) give the following areas within the 200 m contour:

Yellow Sea and East China Sea	977,000 km^2
"Asiatic Mediterranean"	4,715,000 km^2

The former figure agrees well with the figure used here, but the "Asiatic Mediterranean" figure (apparently not defined precisely) is rather greater than the total of the areas above (omitting Yellow Sea and East China Sea) (=4.17 million km^2). Moiseev (1969) gives a figure of 4.5 million km^2 for the whole region.

2. HYDROGRAPHY

The Western Central Pacific is dominated by the Equatorial Current system and even in southeast Asia the area is under greater influence of Pacific than Indian Ocean waters (Wyrtki 1961). A general view shows a striking difference between the northern and southern sections. In the north, the circulatory pattern is relatively constant with the strong Kuroshio Current the dominant feature; to the south the surface currents are greatly influenced by the prevailing monsoons. Many of the currents in the southern waters alternate in flow direction in response to changes in wind direction, i.e. during one part of the year the surface water flow is in one direction and during the other part of the year the flow is in the reverse direction (see figures).

The North Equatorial Current flows westward, generally north of 5°N lat., and upon approaching the Philippines separates into two branches, one directed in a general northward direction and the other in a southerly direction. The northern branch moves northward along the Philippine Islands, then along the coast of Formosa where it becomes known as the Kuroshio Current.

The southern branch, depending on the time of year, provides Pacific water into southeast Asia and also forms the basis of the Equatorial Countercurrent.

The Kuroshio moves in a northeasterly direction past the Ryukyu Islands then veers eastward, then northeastward along the coast of Japan up to approximately 35°N lat. Here the Kuroshio leaves the Japan coast and moves eastward as the Kuroshio Extension. In the Ryukyu area the Kuroshio Current sends a branch northward as the Tsushima Current. The major flow of the Tsushima Current enters the Japan Sea, while a part of the flow is deflected north-westward by the tip of Korea into central East China Sea and the Yellow Sea.

The Yellow Sea and East China Sea are characterized by pronounced seasonal changes. During the winter season, cold air moves from the Asiatic continent over these two bodies of water at an average wind speed of 2.5 m/sec. The overall cooling of surface water and the following convection allows an equalization of the temperature of sea water from the surface to the bottom, and the strong successive blowing of cold winds by the continental high atmospheric pressure accelerates the southward advection of cooled water mass from the Yellow Sea to the East China Sea. That is to say, the enlarging of the "Yellow Sea Cold Water Mass" is recognizable. Sea surface temperatures are low, ranging from about 1°C in the north end of the Yellow Sea to 15°C at 30°N lat., 127°E long. in January. The circulation of surface water during the winter season is in a counterclockwise direction. Water of Kuroshio origin moves northward along the eastern side of the East China Sea into the Yellow Sea. Cold surface water from the northern sector of the Yellow Sea is carried southward along the western side and leaves the East China Sea through the Formosa Strait.

During the summer season, the winds blow from the southeast at an intensity comparable to the winter period. The sea surface temperatures are relatively high, ranging from 25°C in the northern Yellow Sea to 28°C in the southern sector at about 30°N lat., 127°E long. in August. The circulatory pattern in summer is not as well defined as in the winter season. Warm water of Kuroshio origin is still deflected northward along the eastern part of the East China Sea and Yellow Sea. Along the western side, rather than a strong southerly flow as noted during the winter period, there is a general northward flow and a considerable amount of South China Sea water moves into the East China Sea.

Besides the current system just mentioned above, another important aspect of the hydrography of these seas is the remarkable tide which is particularly strong at the western coast of Korea—the range between the high and low tides is about 9 m in some places.

As indicated earlier, the circulation of surface waters in southeast Asia is complex with a complete reversal in direction of many of the currents. It is beyond the scope of this paper to describe in detail the complex nature and dynamics of this circulation. Rather it should suffice to describe the prevailing conditions during the peak of the two periods, the north monsoon in February and the south monsoon in August.

In February, the high pressure system located over the Asiatic continent is fully developed. North of the Equator the northeast monsoon prevails (Fig. I1); at the Equator the winds blow from a northerly direction and from south of the Equator to 10°S lat. the winds originate from a northwest direction. The southeast trades blow south of 10°S lat. Since the axes of the bodies of water in southeast Asia generally follow the direction of the wind system, the currents tend to flow in the same

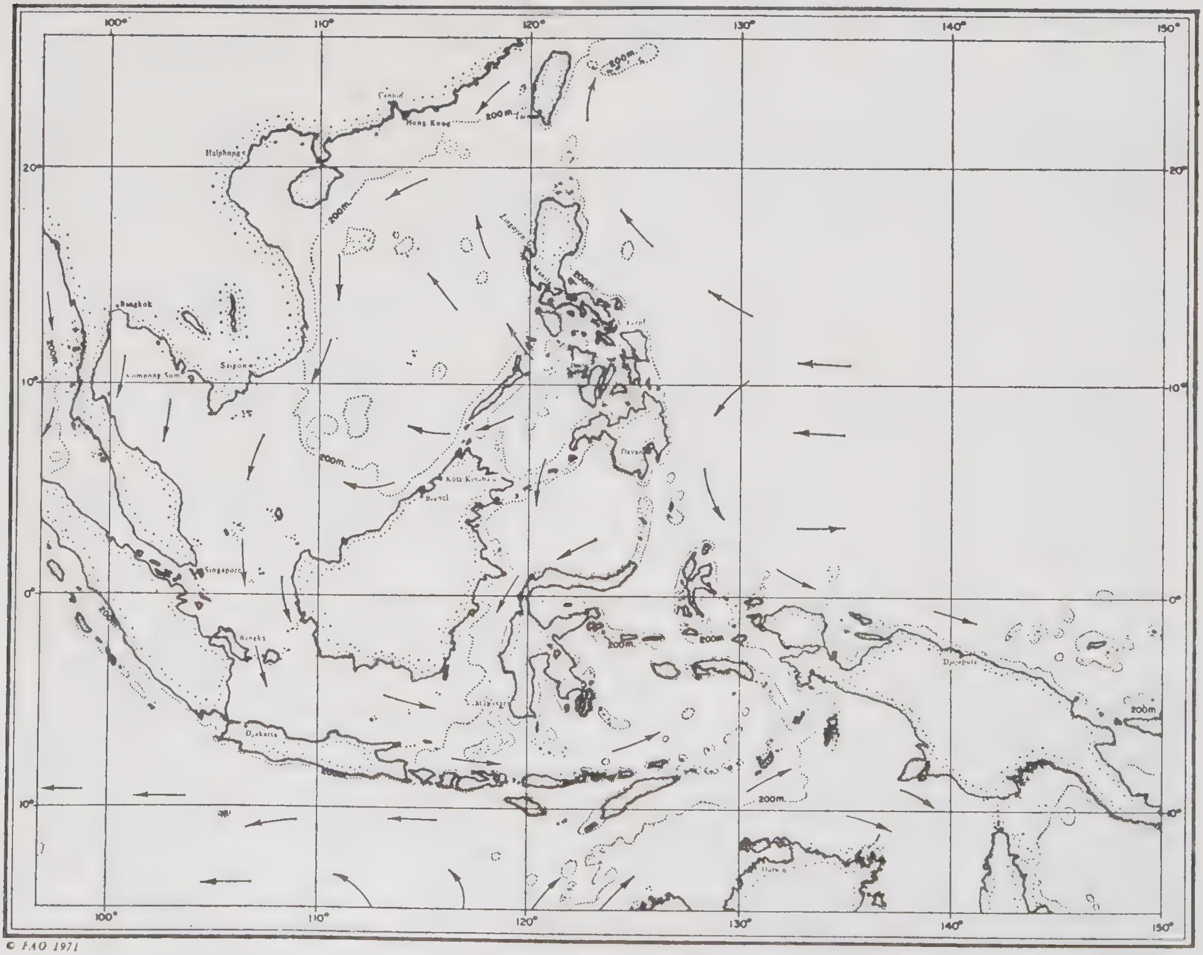

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Fig. I.1. Surface currents in the Eastern Central Pacific in February

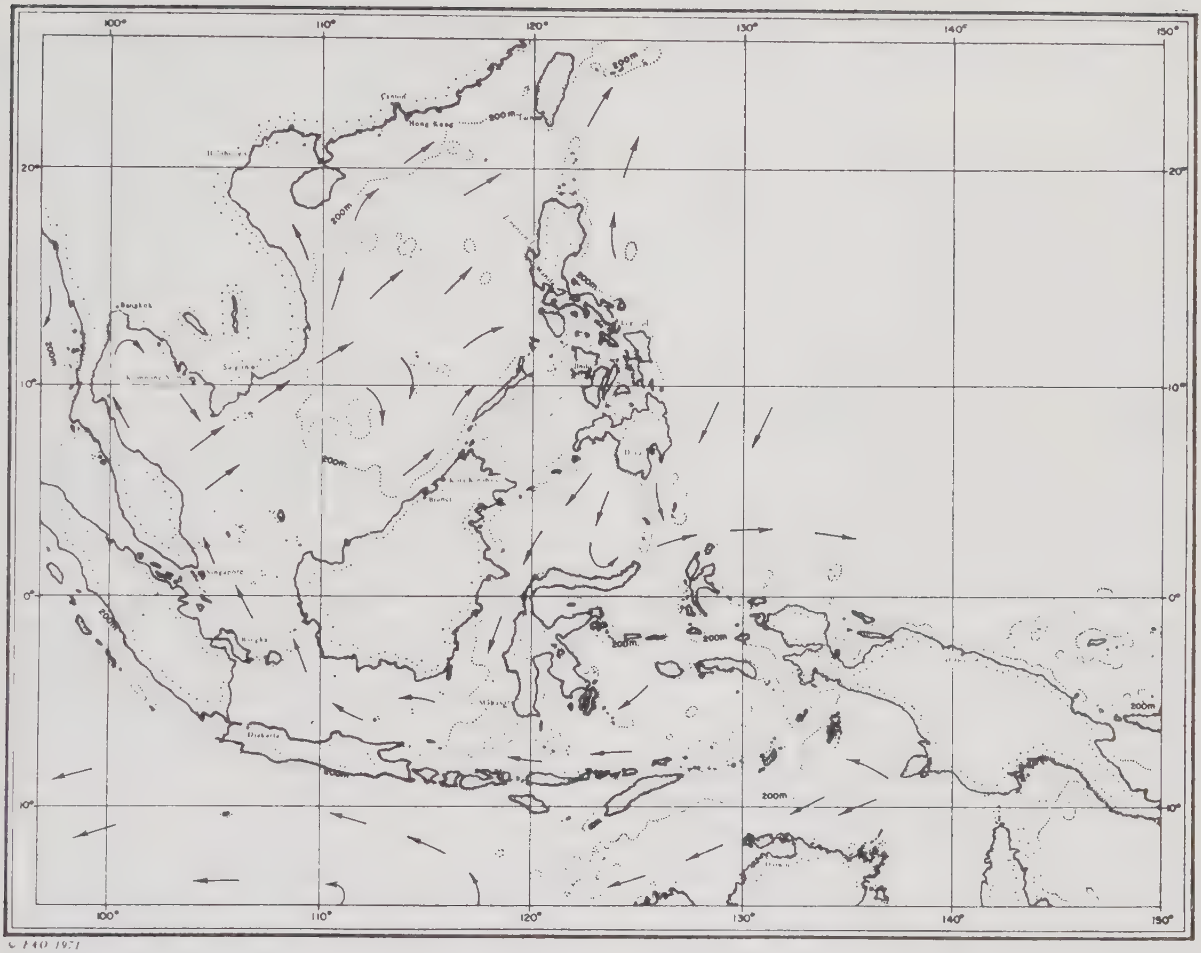

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Fig. I.2. Surface currents in the Eastern Central Pacific in August

direction as the prevailing winds. Figure I1 shows the general surface water circulation in February. North Equatorial water moves into southeast Asia through the south of the Philippine Islands. Along the Asiatic mainland, the currents in the South China Sea area move along the coast in a southerly direction and much of this surface water enters the Java Sea. In the Java Sea the winds are from the northwest and the currents also move in this direction with the flow moving from the Java Sea into the Flores Sea and then the Banda Sea. Part of this water enters the Indian Ocean primarily as southwesterly current in the Timor Sea just south of the Timor Islands; lesser amounts enter the Indian Ocean through the Strait of Malacca and the Sunda Strait.

In August, the South Equatorial Current is strongly developed (Fig. I2) and inflow of Pacific water into southeast Asia occurs south of Mindanao in the Philippines and south of Halmahera Island. A very strong current flows in a northwest direction north of New Guinea and forms the principal water source of the Equatorial Countercurrent. The general surface circulation in the southern seas is from the Banda Sea into the Flores Sea and then into the Java Sea. The Banda Sea receives mostly Pacific water from the northeast. In the South China Sea the flow of water is northward along the continental shelf. During this period there is considerable flow of Pacific Ocean water into the Indian Ocean through the Timor Sea.

2.1 Upwelling

Undoubtedly much of the productive fisheries along the continental shelf of the Asiatic mainland result from nutrients brought up to the surface by the alternating shift in currents and localized regions of upwelling. Available oceanographic data from the western side of the South China Sea indicate localized areas of upwelling off the coast of Vietnam in June and July (Wyrtki 1961). Other areas of possible upwelling include off the coast of Macassar during the southeast monsoon and localized upwelling along the coast of China near Hong Kong during the northeast monsoon and also off the coast of Sarawak.

On the basis of upwelling, the area with the greatest potential of enrichment in southeast Asia is the Banda Sea—Arafura Sea area. Wyrtki (1961) indicated that this was an area of alternating upwelling and sinking and that during the upwelling period, which reaches a peak in July and August, the flow of upwelling water is approximately 5 million m^3/sec.

3. ZOOPLANKTON

In the northern sector, the waters in and south of the Kuroshio are rather barren. The biomass (measured by the net weight of the upper 100 m) is usually less than 25 mg/m^3, with a maximum of 50 mg/m^3 in summer, and in the winter the biomass is usually 25–50 mg/m^3, with a maximum of 100 mg/m^3.

The main species south of the Kuroshio are *Undinula darwini*, *Calanus minor* and *Eucalanus subtenuis*; north of the Kuroshio, *Calanus helgolandicus* is one of the dominant species. (By Motoda and Marimo, Proceedings of Symposium on the Kuroshio 1965).

In the southern sector, studies of zooplankton in Australian waters showed a relatively high standing crop, averaging about 100 mg/m^3, over the Australian continental shelf. In the open ocean the standing crop was considerably lower with values no greater than 50 mg/m^3, usually less than 25 mg/m^3 (Tranter 1962).

4. BENTHOS

The dominant groups in the Yellow Sea and East China Sea are as follows: Holothuridae, Macrura, Brachyura and Cephalopoda in the central part of the East China Sea, with Ophiuroidea in the northern part; Macrura, Ophiuroidea, Brachyura and Asteroidea in the southern part of the East China Sea.

Ophiuroidea are distributed in depths between 60–85 m; Asteroidea in 50–80 m and 100–150 m; Macrura in 50–110 m; Gastropoda and Cephalopoda in about 50 m. In general the peak of the distribution lies about 70 m deep.

Studies of benthos biomass in two bays in the Philippines showed considerable differences in composition and magnitude (FAO, 1959). In Manila Bay the standing crop of benthos biomass was found to be only 0.741 g/0.1 m^2 compared to the 7.957 g/0.1 m^2 for San Miguel Bay. In the Manila Bay samples the dominant groups included errantian polychaetes, macrurans and brachyurans. The major groups in San Miguel Bay were sedentarian polychaetes, errantian polychaetes and ophiuroids. The benthos standing crop of Manila Bay (area of 1,350 km^2) was estimated to be 10,000 metric tons (74.1 kg/ha) and the San Miguel Bay (area of 520 km^2) 40,000 metric tons (795.7 kg/ha).

5. FISH STOCKS AND FISHERIES

5.1 The fisheries

The region is one of the more productive areas of the world, though the large scale industrial fisheries with big ships, concentrating on a few species, characteristic of temperate waters, are absent. Instead the fisheries in the region are typically carried on by a very large number of small vessels, using a wide range of gears, and catching a great variety of species, which are usually not identified (at least down to a species level) on the fish market.

Little or no long range fishing is done in the area, except for tuna fishing in the open Pacific, but all countries in the area have a more or less vigorous local fishery supplying a strong home demand. The most striking recent development has been the growth of trawl fishery by Thai vessels, triggered off by the introduction of single-boat trawling instead of the former pair-trawling. The larger Thai trawlers are now becoming engaged in medium range fishing in the southern part of the Gulf of Thailand and beyond. Medium range vessels also operate from Japan, in the Yellow Sea and East China Sea, and from China (Taiwan) and Hong Kong in the South China Sea.

5.2 Statistics

Recent catches by countries in the area, as available to FAO, are summarized in Appendix Table I8. Except for Japan, the statistics are of total marine fish catch, which in some cases (e.g. Thailand Malaysia and Indonesia) include catches taken outside the present area.

(a) **Japan**

Statistics are generally good, and much detailed data are published in various forms. Detailed breakdown of landings is available from home landings, of which two areas—southern Pacific coast, and East China Sea—come within the region considered here. There is a good breakdown by species and type of gear and fair statistics of effort.

(b) **South Korea**

Statistics are now good (large annual Yearbook of Fishery Statistics published), with the probable exception of coastal subsistence fishing. Area breakdown is available by province of landing; those on west and south coasts come within this region. Breakdown is given by species and type of gear. Effort statistics are not very complete.

(c) **North Korea**

No figures are available since 1957 (then 291,000 tons). Before the war, rather more than half the total Korean catch (925,000 tons out of 1.769 million tons in 1936) came from the present North Korea. Much of this catch was sardine and this stock has very greatly declined. It is probable that the North Korean catch has increased since 1957. There are no details of species breakdown, or of area of capture (especially division between east and west coasts).

(d) **China** (Mainland)

There are no good statistics available. The most recent statistics given in FAO Yearbook are a total of 5.8 million tons in 1960, without detailed breakdown. Shindo (1964) gives a good description of Chinese fishing; of the 5.8 million tons reported, only 1.8 million tons was from normal sea fisheries; the rest being inland fisheries (2.8 million tons) and fish culture (1.2 million tons). These figures are far from being entirely reliable, but the value of marine fish catch seems reasonable in comparison with the length of coastline, and the catches of adjacent countries, such as China (Taiwan) and Korea. Shindo also gives some details of the expansion of marine fishing from 1949 to 1960, as well as the species and area breakdown in 1960. In a later study, in 1966, Shindo re-estimated the marine catch as 1.6 million tons, 1.2 million tons in the Yellow Sea and East China Sea, and 400,000 tons in the South China Sea. It is not known how the Chinese fishery has developed since 1960, but the marine catch is believed not to have increased much.

(e) **China** (Taiwan)

Statistics for this region are generally good; detailed breakdown by species is available.

(f) **Hong Kong**

Good statistics are available for landings in Hong Kong, but much of the fleet land part of their catch (for licensing purposes) in China (Mainland), and this part is not recorded. Detailed breakdown by species is given. Effort and some data are available for some of the large vessels.

(g) **Democratic Republic of Vietnam**

Latest statistics in FAO are for 1962, and their reliability is unknown. The total fish catch is only broken down into marine and freshwater. Between 1955 and 1962, the reported catch increased from 94,000 to 289,000 tons.

(h) **Republic of South Vietnam**

Up-to-date statistics of total catch are available, broken down into freshwater fish, marine fish and crustaceans, in the FAO Yearbook of Fishery Statistics (YFS). The reported totals increase steadily from 120,000 tons in 1955 to 375,000 tons in 1965, but it is not certain to what extent this represents a real increase in catch, or merely greater completeness in the collection of statistics. Probably there are still very incomplete data as small-scale subsistence fisheries are prevalent in both fresh and coastal waters.

(i) **Khmer Republic (Cambodia)**

Catch statistics are given in the FAO Yearbook for 1961/5 with sub-totals for freshwater fish, marine fish, crustaceans, molluscs and various. The totals show a very slight increase (from 148,000 to 166,000 tons) but it is not known how reliable these figures are. There is probably a great deal of under-reporting of subsistence fishing.

(j) **Thailand**

Detailed statistics are available, though the figures include a very large proportion of unsorted and unidentified fishes (probably mostly from the rapidly developing trawl fishery). It is known that part of the rapid increase in the total reported catch since 1961 is due to improvement in the collection of statistics. Probably the most recent figures are reasonably reliable.

(k) **Malaysia and Singapore**

Detailed statistics by species are available. These are probably reasonably reliable. Some effort data are available for major fisheries.

(l) **Indonesia**

The reliability of the figures (1.176 million tons of marine and freshwater fish reported in 1968) is probably very low. The figures are more likely to be too low than too high because of non-reporting of subsistence fishing. Of the 1967 total (1.18 million tons) approximately 640,000 tons were believed to be marine fish. Nearly all the catch is taken by small boats in depths less than 25 m, not more than 25 mi from shore.

(m) **Australia**

There is very little fishing in the region. A shrimp fishery is developing in the Gulf of Carpentaria for which good statistics should be available.

(n) **New Guinea, Solomon Islands, other island groups**

There are very little data available, most of which are of export figures only. The latter are probably reliable, and the total catch is probably small.

(o) **Philippines**

The FAO Yearbook gives detailed figures, broken down by species; much of these data have been derived from information which might be used for tax purposes, adjusted by a factor believed to correct for misrepresentation. The factor used may be too large or too small. The proportions of different species may be a reasonably reliable estimate for the commercial fisheries, but these proportions may not be the same in the so-called municipal fisheries, which account for about half the total reported catch. Probably demersal fish are commoner and pelagic fish rarer in the municipal catches than the published statistics suggest.

(p) **Long-range fishing**

Fortunately, in view of the deficiencies in the statistics of local fishing, there is not much long-range vessel fishing in the region far from the home bases. Japanese trawlers have occasionally worked in the South China Sea and the Gulf of Tongking, and there may be developments in long distance trawling and fishing for shrimps in the South China Sea by Korea, Hong Kong, Thailand and Singapore, but this is likely to remain on a small scale. High seas fishing for tuna is considered separately in the section on oceanic resources. The main statistical problems are, therefore, confined to the countries adjacent to each area concerned.

5.3 Stock assessments for exploited stocks

(a) Yellow Sea and East China Sea

Demersal

Assessments for the major stocks have been carried out by Japanese scientists. These studies have shown some degree of separation of discrete stocks within the area. However, the degree of exploitation of different stocks of the same species seems much the same. There is not much information of the degree of mixing with stocks outside the region; however, the demersal fish do not seem to migrate far. The analysis for demersal fish covers the area of the Japanese trawl fishery; this extends south to about 26°N, and therefore covers nearly the whole of the East China Sea areas as used here.

The present demersal catch from the area is uncertain; from Shindo (1964) the catch of marine fish by Mainland China in 1960 was 1.8 million tons; of this, two-thirds came from the area considered, and the great majority of this total was demersal fish. Allowing for a slight increase since 1960, the 1965 catch of demersal fish may be estimated as 1.2 thousand tons. The Taiwan catch in 1965 consisted of 84,000 tons of specified demersal fish, and 61,000 tons of unspecified fish, probably nearly all demersal, i.e. a total of 145,000 tons; the proportion of this that came from the East China Sea is not known, perhaps it is as much as one-third, say 50,000 tons. The Japanese and South Korean catches are known reasonably well. It is not known what proportion of the North Korean catch is demersal fish, nor how the total is divided between the East (Japan Sea) and the West (Yellow Sea) coasts, but probably most of the catch is taken in the Japan Sea. The best estimate of the total demersal catch in the Yellow Sea and the East China Sea is as follows:

TABLE I2. DEMERSAL CATCHES IN THE YELLOW SEA AND THE EAST CHINA SEA

Area	*Estimated catch 1965 (in metric tons)*
Mainland China	1,200,000?
Japan	330,000
South Korea	130,000
Ryukyu	1,000
Taiwan	50,000
North Korea	100,000?
Total	1,810,000

A major uncertainty remains concerning the share of the total taken by Mainland China (Shindo 1964). The evidence of decline in catch per unit effort, smaller sizes of fish, and increased mortality show clearly that the demersal fisheries are approaching or beyond the level at which no further increase in average catch can be achieved. (See Anon. 1963, Mako 1961, Murakami *et al.* 1964 for demersal stocks generally; Misu 1965 for ribbon fish (hairtail), *Trichiurus lepturus*; Ikeda 1964 for yellow croaker, *Pseudosciaena manchurica*; Otaki 1964 for sharp toothed eel, *Muraenesox cinereus*; Shindo 1964 for yellow sea bream, *Taius tumifrons*). The trends since 1953 in catch and catch per unit effort for different species have been different; some tending to increase, e.g. ribbon fish and shrimp, at least up to 1961, while others have decreased sharply, e.g. lizard fish (Murakami *et al.* 1964). Most recently the catch per unit effort even of those species which had been increasing have tended to flatten out or decrease. These differences are probably due to several causes, including:

(a) changes in the balance of species in the sea, independent of fishing;
(b) relative decreases of species most vulnerable to fishing;
(c) switching of the main fishing concentration from the initially preferred species;
(d) development of new fisheries, e.g. for shrimp.

Because of these differences, it is most unlikely that the intensity of fishing is the same for all stocks, and while all the demersal stocks included in the above analysis are at least moderately heavily fished, it is likely that the yield of some could be increased by heavier fishing, while the yield of others could be increased by reduced fishing. In addition, the yield of several species might be increased by the use of larger trawl meshes. Potentially, therefore, the yield of the presently exploited demersal fish could be increased (perhaps by 10–30%), but much of this increase would require rather detailed control of fishing. It is probably unrealistic to expect much change from the present total. A potential yield of 2 to 2.4 million tons corresponds to a yield per unit area of *c.* 25 kg/ha.

Pelagic

Estimates of the present yields of pelagic fishes from the Yellow Sea and the East China Sea are provided in the following table. The figures for Mainland China and North Korea are both very rough, assuming about one-third of the Korean catch are pelagic fish, but, following Shindo (1964), that the pelagic catch by China is small, say 10% of the total.

TABLE I3. PELAGIC CATCHES IN THE YELLOW SEA AND THE EAST CHINA SEA

Area	*Estimated catch 1965 (in metric tons)*
China (Mainland)	100,000?
Japan*	350,000
South Korea	100,000
China (Taiwan)†	20,000
North Korea	100,000?
Total	*c.* 600,000?

* Jack mackerel and mackerel
† Assuming East China Sea catch is one-third of total

Studies have been made by Japanese scientists of the major species. The two species of mackerels (*Scomber japonicus* and *S. tapeinocephalus*) are mixed in the statistical records. While catches have recently increased very greatly in other parts of Japan, the catches in the present area have not changed much. Effort and catch per unit effort data also show little change, but the effort figures do not take into account improvements in the gear efficiency. Size and age distributions show a dominance of small, young fish. It is, therefore, believed that the stock is heavily fished (Tsujita 1965), though the evidence is not as conclusive as for the demersal fish.

Catches of jack mackerel (*Trachurus japonicus*) increased in 1958/60 due to an expansion of Japanese fishing in the East China Sea, and probably also a greater availability of the stock. Since then, catches and catches/effort have been more stable, but efficiency of the unit of effort may have increased. Average age and size is low (Mitani and Shojima 1966) and may be decreasing. There is some indication of the existence of different stocks.

Though the situation is not as clear as for demersal fish, it is the belief of Japanese scientists that these stocks are heavily exploited and catches from them cannot be substantially increased by greater fishing. Pelagic catches in Japanese waters have fluctuated very greatly, probably largely independent of fishing.

Japanese scientists have data on larval abundance of several pelagic species. It is hoped to examine these to obtain estimates of relative (and perhaps absolute) abundance of these species.

The food items of a species forming the base of large fisheries often provide clues to potential resources of unexploited species. Stomach contents of ribbon fish (*Trichiurus lepturus*) contained the following relative numbers of different species of fish (in brackets catch in tons from the area by Japanese and South Korean vessels) (Misu 1964).

Engraulis japonica	118	(95,000)
Trichiurus lepturus	60	(70,000)
Pseudosciaena manchurica	50	(70,000)
Argyrosomus argentatus	11	(25,000)
Other identified fish	42	

It is interesting that anchovy is the only pelagic fish taken by ribbon fish. These studies do not suggest the existence of any substantial unexploited stocks. The potential yield is probably not much more than the present total catch, perhaps 25–50% above it, i.e. three-quarters to one million tons.

(b) **Other areas on continental shelf**

Little stock assessment work has been carried out and in many areas even the basic data on catches, effort, sizes, etc. are lacking. Some data are being collected in Taiwan, Hong Kong, Thailand, Malaysia and Philippines and assessments are now available for some of these fisheries.

Demersal

South of the East China Sea area, trawling takes plac along the Asiatic continent, with increased effort noted in waters around Hong Kong, Gulf of Thailand and the Philippines. More recently trawling has increased in the Strait of Malacca by Malaysia and exploratory work is being intensified in the southern sectors of the South China Sea by various countries, e.g. Taiwan and Thailand. The present fish catch from these southern waters is given below:

In the area off the south coast of China, between Taiwan and Hainan, there have not been detailed stock assessments, but experience from Hong Kong suggests that there has been an appreciable falling off in the catch rates, at least of the preferred species. This suggests that the potential yield of demersal fish in the area is being approached, i.e. that the potential is probably in the range of 800,000 to 1.5 million tons.

In the Gulf of Thailand, the recent rapid increase in trawling has been followed by a substantial fall in catch per unit effort (Isarankura and Kühlmorgen-Hille 1967, Tiews *et al.* 1967). Some further increase in catch may be possible. It appears that a large variety of species is caught and landed, though only half the catch is of fish used for human consumption (Tiews 1966). Probably all species easily taken by the present gear are exploited, if not to precisely the same extent.

An assessment of the demersal stock in the Gulf of Thailand has been made by Gulland (in press), using data on total catches, number of vessels and catch per unit effort of survey vessels given by Menasveta (1968). The last has decreased from just under 300 kg/hour in 1960 to 115 kg/hour in 1967. Making some allowance for the spread of fishing into more distant waters, so that only a proportion of the total catch in recent years comes from the survey areas in the northern part of the Gulf, there appears to be a clear and approximately linear relation between the survey catch per unit effort and the total effort. The corresponding relation between total catch and effort gives a maximum yield of 400–500,000 tons per year at a level of fishing rather less than that in 1966. Since 1967 the total catch by Thai trawlers has increased above half a million tons, but this increase has come from trawlers moving into more distant areas. An estimate of 500,000 tons as the potential of the area directly off the Thai coast still appears the most reasonable, if some allowance is made for a small increase in catch from more selective methods of fishing.

This analysis did not take into account the changes in species composition that have taken place (Tiews *et al.* 1967). Some of these changes are the direct effect of fishing, e.g. the greater decline of the larger or more valuable species; others can be ascribed to the indirect effects, e.g. the increase in squids due to the reduction in their predators. Other changes, e.g. the increase in *Lutjanus*, which being a large valuable fish might have been expected to decrease greatly, are less easily explained. They may be due to complex fishery-induced causes, or

TABLE 14. ESTIMATED DEMERSAL CATCHES BY AREAS (IN 1966)

Area	*Catch by countries*		*Total (in metric tons)*
Formosa Strait and Chinese South Coast	China (Mainland)	550,000	
	China (Taiwan)	100,000	
	Hong Kong	50,000	700,000
Gulf of Tongking	China (Mainland)	50,000?	
	Vietnam Dem. Rep.	200,000?	250,000
South China Sea	Republic of S. Vietnam	250,000? (total marine fish 290,000)	
	Malaysia	75,000	
	Singapore	10,000	
	Indonesia	10,000	400,000?
Gulf of Thailand	Thailand	337,000	
	Khmer Republic	30,000 (total marine fish 40,000)	370,000
Java Sea	Indonesia	500,000?	500,000?
Gulf of Carpentaria and Arafura Sea	Australia	negligible	
	Indonesia	?	probably very small

may be completely independent of fishing. Any full analysis of the changes in the demersal fish community must, therefore, be a rather involved study. It may well be that short of an extremely detailed study, the simple study above, in which the total catch per unit effort of the survey vessels may be taken as a synthesis of all the direct and indirect effects of fishing, gives a rather better assessment of the state of the stocks generally than a species-by-species analysis.

This is only the sustainable yield from the part of the survey area fished by Thai trawlers, which is not the same as the whole of the Gulf of Thailand. Tiews stated that fishing is not carried out below 50 m, and considered the catches at that time came from an area of 24,400 n.mi^2 (= 84,000 km^2). This is not much more than a quarter of the total area of the Gulf less than 200 m as estimated in the first section (=89,000 n.mi^2 = 305,000 km^2). Use of one or other of these areas gives values of yield per ha of 60 and 17 kg/ha respectively (6.0 and 1.7 tons/km^2 respectively). Though high, a figure of 60 kg/ha may be compared with annual catches of 20–25,000 tons from Manila Bay (150–180 kg/ha) (Tiews 1959). This figure includes some pelagic fish, and also includes fish caught inside the Bay which have grown up outside the Bay. It may therefore be an over-estimate of the harvested production of demersal fish per unit area, though some studies by the FAO/UNDP(SF) project suggest that the true demersal catches in Manila Bay may be as high as 30–40,000 tons, and suggest that this production can be quite high.

As an estimate of the productivity from all waters, the latter figure (17 kg/ha) will certainly tend to be an under-estimate because much of the fish in deeper waters, or in the south-eastern part of the Gulf (off Cambodia), will not move into the area fished by Thai trawlers; equally the former figure (60 kg/ha) may be an over-estimate of the productivity in waters shallower than 50 m, because the catches may include fish which have moved into the fished area, and therefore represent the production over a bigger area than considered by Tiews. There are no good data for productivity in waters deeper than 50 m. Data from several areas (Tiews 1966, Pathansali *et al.* 1967, etc.) show that trawl catches are much less in deeper waters, at least in some areas. Exploratory fishing data from the FAO/UNDP project in the Philippines, provided by J. Magnusson, show little difference in catch rate—*c.* 200 kg/hour—in 50–100 m, and in less than 50 m. However, the deeper water is at present little exploited, and the similar catch rates may reflect lower productivity, plus lower exploitation.

Therefore, it is best to follow Tiews in assessing the possible catches in waters less than 50 m deep separately; for this the higher figure above is probably closer to the value for the Gulf of Thailand. A likely range may be between 30 and 50 kg/ha (3–5 tons/km^2). If the other tropical and sub-tropical areas in the Indo-Pacific region shallower than 50 m, which, according to Tiews (1966), cover 465,000 n.mi^2 (= 1.6 million km^2), were as productive as the Gulf of Thailand, the total potential catch of demersal fish would be between 4.8 and 8 million tons. However, if the waters of the Gulf of Thailand shallower than 50 m are more productive than other parts of the region, this may be an over-estimate. There is evidence that this is so, e.g. Ichiye (in Fairbridge 1966) quotes figures of primary production of 6 gC/m^2/day at the head of the Gulf, 1–2 gC/m^2 in the central part, compared with 0.5 gC/m^2 in Philippine off-shore waters and the Celebes Sea. However, productivity round the Phillippines appears to increase towards the shore and to be exceptionally high in Manila Bay.

The relative potential of demersal fish in different areas may also be estimated from a comparison of actual trawl catches, by commercial, exploratory, or research vessels. This has to be done with some caution, since trawl catches depend very much on the size and power of the vessel, type and rigging of the net, time of day etc. However, an increasing number of observations are now becoming available for the region. Besides covering an increasing proportion of the potential trawling area, there should be an increasing overlap in which more than one ship has fished in the same area at the same time of year, thus providing a proper opportunity for inter-ship calibration.

Lester (1967) and Menasveta (1968) have reviewed most of the published data in the Sunda Shelf area, the most important of which are the surveys carried out from Taiwan (Tsung 1962; Yee 1961, 1963; Tseng (1967), though other surveys have been made from Malaya (Ommanney 1961), Hong Kong and Thailand (Tiews 1966). Four areas produced good catches; in the Taiwan surveys the highest catches were on the east side of the Gulf of Thailand, and South Vietnam (15 boxes, or *c.* 400 kg/haul), followed by the area off the Mekong (12 boxes, or *c.* 300 kg/haul), and the northern part of the Gulf of Thailand (7 boxes, or *c.* 200 kg/haul); other vessels also took good catches round Natuna Island, in the centre of the Sunda Shelf. These results confirm the higher potential of the inner Gulf of Thailand, especially since this area was, at the time of the surveys (1960/4), more heavily exploited than others.

However, the surveys also showed that demersal fish were present over the whole of the Sunda Shelf. Blank hauls occurred, as they do in all fishing operations, but there was no large area of consistently zero or very low catch. Excluding the richer areas noted above, the average catch per haul in the Taiwan surveys was 4 to 5 boxes (100–125 kg). This is perhaps half the value that would have been obtained in the inner Gulf before fishing started; probably the potential yield is in proportion to the standing crop. Reasonable estimates for the potential yield are, as extrapolated from experience in the Gulf of Thailand, therefore, 20–30 kg/ha in the richer parts, and 15–25/ha, elsewhere. These figures may be compared with the fairly good estimate of *c.* 25 kg/ha in the East China Sea, and the much rougher estimate of 800,000–1.5 million tons total, or 30–50 kg/ha for the Chinese south coast. The agreement is reasonably good, and using these figures, estimates of demersal potential may be summarized as shown in Table 15.

The total demersal potential as estimated in this table is 9.1–13.3 million tons. This is about double the present catches, though the immediate prospects for expansion are not quite as good as this two-fold difference implies, since some of the areas where the unexploited potential is greatest are the open areas of the South China Sea, some distance from suitable markets, and where the

Table 15. Estimated demersal resources of the Western Central Pacific by areas

	Area ('000 km²)	Present catches ('000 tons)	Catch, kg/ha Present	Catch, kg/ha Potential	Total potential ('000 tons)
Yellow Sea—East China Sea	950	1,800	20	25	2,000–2,400
Chinese south coast	280	700	25	30–50	800–1,500
Gulf of Tongking	200	250	12	30–50(a)	600–1,000
Gulf of Thailand					
Thailand coast	84	337	40	60	500
Southeast coast	50	50?	10?	60(a)	300
Central	170	—	—	15–25(a)	250–400
South China Sea					
Richer areas (b)	50	?	?	30–50(a)	150–250
Others	920	?	?	15–25(a)	1,400–2,300
Java Sea	580	500?	9?	15–25(a)	900–1,500
Gulf of Carpentaria	960	—	—	15–25(a)	1,500–2,500
Philippines (c)	215	200(400?)	10	30–50(a)	600–1,000
New Guinea, etc.	90	?	?	15–25(a)	135–225

Notes: (a) Extrapolated from Gulf of Thailand.
(b) Off the Mekong Delta and Natuna Island. Other areas may later be shown to be rich, so the figures for the whole South China Sea may be an under-estimate.
(c) Studies by the FAO/UNDP(SF) project suggest that the true demersal catch may be as high as 400,000 tons, and the pelagic catch rather less than reported.

catch rates are low, and consist of a large proportion of low-valued fish.

Pelagic

Estimates of the present yield of pelagic fish from the southern waters are provided in the following table. As indicated earlier, the lack of data from many localities in this area subjects the estimates of present catches to considerable error.

The best studied area is probably again the Gulf of Thailand and virtually all the Thai catch (of some 70,000 tons) came from north of 9°N (statistical areas I, II and III). The stock has been studied in detail in a report by Kurogane *et al.* given to the 1970 session of the Indo-Pacific Fisheries Council. This concluded on the basis of a careful analysis of catch and effort data, size composition information and tagging results that no great increase in catch could be achieved either by an increase in effort, or by a change in size at first capture. Allowing for additional catches from the southern part of the Gulf of Thailand, if the fish there are a separate stock, it seems that the potential catch of pelagic fish from the Gulf is probably 100,000 tons, and may well be as much as 200,000 tons and might even be greater.

The pelagic resources in the Gulf are, therefore, probably rather less than the demersal resources, but probably rather more than a quarter of the demersal fish. Lacking better data, it is reasonable to assume this is also true of other areas in waters less than 50 m, which would give a total pelagic resource in the shallow water zone of from 1 million tons, as a conservative lower limit, up to perhaps 5 million tons.

In deeper waters (between 50 and 200 m), the pelagic fish are probably relatively more abundant; the large area concerned implies that the total demersal stock may be quite large, even if too widely scattered to be at present commercially exploitable; and the pelagic resources are probably as large or larger. A total resource of 1 million tons from this zone would imply a value of only 4 kg/ha (0.4 tons/km²), about one third of the lower

Table 16. Estimated pelagic catches, by areas in 1966 (in tons)

Area	Catches by countries		Total
Formosa Strait and China south coast	China (Mainland)	100,000?	
	China (Taiwan)	50,000	
	Hong Kong	10,000	160,000?
Gulf of Tongking	China (Mainland)	10,000?	
	Dem. Rep. of Vietnam	100,000?	100,000?
South China Sea	Rep. of S. Vietnam	70,000?	
	Malaysia	20,000(a)	
	Singapore		
	Indonesia	10,000?	100,000?
Gulf of Thailand	Thailand	70,000	
	Khmer Republic	10,000	80,000
Java Sea	Indonesia	300,000?	300,000?
Gulf of Carpentaria	Australia	negligible	
	Indonesia	?	?
Philippines	Philippines (b)	300,000	300,000
Total—all southern waters			*c.* 1,000,000

Notes: (a) Most of the Malaysian pelagic catch is taken on the west coast, outside the present region.
(b) True catch may be rather smaller.

estimate of the yield per unit area of demersal fish in the shallow zone. This is not unreasonable.

Island resources

One of the most notable features of the Western Central Pacific area is the presence of numerous islands of volcanic and coral origin. With the exception of relatively fair-sized commercial fishing carried out in the Ryukyu Islands and the Philippines, much of the fishing effort in the island areas is of a subsistence type and directed to fish and shellfish in the immediate coastal waters; primarily in the reef zone. The pelagic waters are presently fished for tunas and billfishes by Japanese, Chinese and other far-ranging fishing fleets. Another group of resources has been recently exploited by Russian trawlers which have taken good catches of bottom and near bottom fishes near some of the mid-ocean islands. While some data are available from these long range fisheries, data are almost completely lacking on the magnitude of the catch resulting from the subsistence type fishing around the islands. Although stock assessment estimates are not available for the fish species around the island waters, there are indications that much of the reef areas are presently over-fished, especially those located close to large communities.

Undoubtedly with proper management the yields of the over-fished reef areas can be increased; however, the total yield cannot be expected to be too great since the reef areas are relatively limited. In island waters, the resources which have not been explored or exploited to a great degree are the fishery resources in deeper waters beyond the reef zones. These waters contain demersal species such as snappers and groupers, and pelagic species of schooling fish such as scads and mackerel. To date these resources have not been fully harvested principally because of inadequate gear and marketing problems.

The estimate of the potential yield of the island waters (excluding the open sea fish species, e.g. tunas and billfishes) provided in the following table were obtained on a basis of comparability with a nearly fully exploited area, the Hawaiian Islands:

TABLE 17. POTENTIAL YIELD FOR ROUND OCEANIC ISLANDS IN THE WESTERN PACIFIC

Area	*Length of coastline (mi)*	*Potential yield (a) (metric tons)*
Nampo Shoto group	153	612
Trust territory of the Pacific Islands	3,561	14,244
Gilbert Islands	626	2,504
Ellice Islands	135	540
Solomon Islands	2,464	9,856
Islands southeast of New Guinea	3,943	15,772
Total	10,882	43,528

Note: (a) Based on yield of 4.0 metric tons per mi of coastline.

The fish fauna of the Hawaiian Islands is similar to the fauna of the Western Central Pacific Islands. The Island of Oahu has a general coastline length of 112 mi and the waters of Oahu are the most intensively fished of the major islands in the Hawaiian chain. The present catch of neritic pelagial fish species around Oahu has been estimated to be 4.0 metric tons per mi of coastline per year. Applying this rate to the island waters (excluding Ryukyu Islands, Taiwan, Philippine Islands, New Guinea and islands to the west of these areas) in the Western Central Pacific provides a rough minimum potential yield of 43,500 metric tons of fish. It is very likely that the true potential yield of fish from the island waters of the Western Central Pacific is some multiple of the 43,500 tons provided here. A three- to five-fold increase is not unrealistic, especially since the fauna of the Western Central Pacific is considered richer than the Hawaiian fauna and there is some evidence that fishing in Hawaii has not reached it full potential. As indicated in the above table, the total coastline of the islands in the Western Central Pacific considered here is estimated to be about 11,000 mi.

6. SUMMARY AND DISCUSSION

6.1 Summary

The estimates of potential in the region are of around 9–13 million tons of demersal fish, and of 2–6 million tons, or quite possibly more, of pelagic fish. These figures are extremely rough, and the range of estimates, though wide, are certainly no wider than the inadequacy of the data. However, the information is good enough to show that there are ample opportunities for expanding fish catches in the region, with the exception of certain heavily fished areas (e.g. the Yellow Sea, and the northern part of the Gulf of Thailand). The estimates also suggest that, especially for demersal fish, the region is potentially one of the most productive in the world, exceeding for example the total potential of the rich but less extensive areas of the Northwest Atlantic by some four-fold.

This is perhaps surprising in view of the fact that the region has not attracted the long distance fleets which exploit such areas as the Northwest Atlantic, Southwest Africa, etc., but may be explained by several factors. First, the shelf area is very large, so that the actual potential per unit area is not estimated to be very high. Secondly, the presumed faster turn-over and shorter life-span of most fishes in these warmer seas prevent the accumulation of large unexploited standing stocks and, under conditions of steady fishing, result in lower mean abundance from a given annual production. Also the wide variety of species in tropical areas is less attractive to industrial operations than the single-species fisheries of higher latitudes.

6.2 Requirements for further study

Although the available data have enabled estimates of potential to be obtained which are useful as first rough guides to the possible developments of fisheries in the area, it is obvious that much improved estimates are desirable.

The primary requirement is clearly an improvement in many of the basic statistics. It is impossible to make any useful estimate of the potential yield if the present yield is not known with any accuracy, and this accuracy is lacking in the available statistics of several countries. For nearly all fisheries there is an absence of any data of fishing effort in any form.

There are very few detailed assessments of the state of stocks and until the basic data, especially the statistics, have been improved, the number of stocks for which good assessments are available must remain small.

For most parts of the area, therefore, estimates of potential yield will have to be by comparison with other, better studied areas. It is, therefore, important to check how valid such comparisons are. This is best done as a comparison of the stock of commercial fish, e.g. as catch per hour of a standard unit of gear, but standardization is not too easy. Any other measure of biological productivity, from primary production onwards, would therefore be most useful, especially from the waters round Indonesia, in which data are very sparse.

Information on pelagic resources and of fish resources generally beyond 50 m depth is also sparse and urgently needs improving. Surveys with modern sonar and echo sounder gear to check on the presence or absence of shoals of pelagic fish (especially if accompanied by an efficient fishing vessel/purse seiner, or mid water trawler) would be particularly useful.

Appendix

TABLE I8. CATCHES FROM THE WESTERN CENTRAL PACIFIC ('000 TONS)

Country	1962	1963	1964	1965	1966	1967	1968	1969
Vietnam (North) (a)	222	214	(215)	(215)	(215)	(215)	(215)	(215)
Vietnam (South)	200	329	345	318	316	351	359	400
Cambodia	31	36	40	43	39	45	46	45
Thailand	249	303	472	513	591	648	842	(1,070)
Malaysia (b)	(170)	(200)	210	220	259	334	372	...
Singapore	11	12	10	11	18	18	17	17
Philippines	429	486	606	668	708	752	878	906
Brunei	2	4	3	4	3	1	2	2
Indonesia	436	447	(450)	(500)	(540)	(508)	534	566
New Guinea	(7)	(10)	(10)	(13)	(13)	(13)	(14)	(14)
Australia	*	*	*	*	*	*	*	1

Notes: (a) Catch of Vietnam (North) is very rough estimate
... No data
Brackets denote estimation
The precise figures of the catches of several other countries should be treated with some caution (see text)
(b) Malaysia excludes Sarawak
* Denotes catches less than 50 tons

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7147

COASTAL AND HIGH-SEAS PELAGIC FISHERY RESOURCES OF THE WESTERN PACIFIC OCEAN

by

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ABSTRACT

This brief review of the coastal and high-seas resources of pelagic fishes in the western Pacific is intended as background material in planning for a symposium to be held in 1972 during the 15th Session of the Indo-Pacific Fisheries Council, and was prepared at the request of the 13th IPFC Session. The area covered in this report includes Japan and Korea in the north and New Zealand, Australia, and the coastal waters of the Indonesian Archipelago in the south. The general features of the fisheries and the hydrography in the western Pacific are discussed. A more detailed review is made of the more important pelagic fishes which include the categories (1) jacks, mullets, etc., (2) herrings, sardines, anchovies, etc., (3) tunas, bonitos, and skipjacks, and (4) mackerels, billfishes, cutlassfishes, etc.

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INTRODUCTION

This brief review of the coastal and high-seas resources of pelagic fishes in the western Pacific was prepared in response to a request made at the 13th Session of the IPFC (Indo-Pacific Fisheries Council) held in Brisbane, Australia, on 14-25 October 1968. The document provides background information needed for the planning of a symposium scheduled to be held in 1972 during the 15th IPFC Session.

Although the IPFC area includes the Indian Ocean, we have focused our attention on the western Pacific and adjacent waters. The recently organized Indian Ocean Fisheries Commission is already undertaking a review of the Indian Ocean fishery resources. The area covered in this report (Fig. 1) includes the waters extending from the Asiatic coast eastward to 180°. For convenience, the northern boundary has been placed along lat. 45°N and includes the coastal waters of Japan and Korea. The southern boundary includes the waters surrounding New Zealand, Australia and the southern part of the Indonesian Archipelago.

In our discussions covering the important coastal and high-seas, pelagic fishery resources of the western Pacific, we have restricted our comments relating to the fisheries of Japan and Korea to those species whose areal distributions extend to southern waters or to fish that have related species in southern waters.

In the following sections we will review briefly the status of fisheries in the western Pacific and the hydrography of the area, and provide details of several of the more important commercial fish species. For the latter, we have followed the general classification outlined in the FAO Yearbook of Catch Statistics (see, for example, FAO, 1969). The pelagic fishes are discussed as follows (1) jacks, mullets, etc., (2) herrings, sardines, anchovies, etc., (3) tunas, bonitos, and skipjacks, and (4) mackerels, billfishes, cutlassfishes, etc. Except for providing figures on total landings, the category of sharks, rays, and chimaeras is not discussed.

SOME GENERAL ASPECTS OF FISHERIES IN THE WESTERN PACIFIC

On the basis of FAO catch statistics (FAO, 1969), the 1968 world catch of fish and other fishery products was 64.0 million metric tons. Table I provides a summary of the catch (based principally on 1968 statistics) for those countries located in the western Pacific. Although precise data are lacking for some of the countries, e.g., Indonesia and mainland China, the estimated total regional catch of 20,849.7 thousand metric tons represents about 33 percent of the total world catch. It should be noted that a substantial part of the catches reported for Japan, Korea and Taiwan come from waters outside of the IPFC area; e.g., approximately 15 percent of the total demersal catch made by Japan was taken in a distant-water trawl fishery.

The growth rates of the fisheries in some of the southeast Asian countries have shown sizeable increases in recent years. Table II which illustrates the growth of the fisheries for a few selected countries, shows increases ranging from 3.5 percent per annum for Japan to a high of 26.0 percent per annum for Thailand. Much of Thailand's growth is attributed to the rapid development of bottom fisheries (Isarankura and Kühlmorgen-Hille, 1967). Even while further expansion of the bottom trawl fishery can be expected, especially in parts of the South China Sea (Menasveta, 1970), the pelagic resources of the coastal and high-seas waters show promise of substantially greater increase in landings, e.g., the present catch from Indonesian waters is estimated to be only 15 percent of the total potential yield (Comitini, 1970). Except for the tunas taken in the high seas by Japan, Korea and Taiwan, much of the pelagic fishes taken in southeast Asian waters come from coastal areas, mainly within 15 miles of land (Comitini, 1970). Shomura and Gulland (in press) in a recent review of the fishery resources of the western central Pacific Ocean estimated the potential yield of pelagic fishes as ranging from 1 to 5 million tons in waters less than 50 m and at 1 million ton in waters from 50 to 200 m.

Within the coastal area itself, there is wide diversity in the degree of fishing intensity and in the fishing gear and techniques used. In some areas, such as off Thailand (Isarankura and Kühlmorgen-Hille, 1967) fishing is intensive, but in other areas such as off New Zealand, Australia and Indonesia, fishing intensity is relatively light. Furthermore, fishing is generally confined to waters within visual distance of shore. While a number of factors contribute to this lack of an expansion offshore, the lack of suitable fishing crafts and the inability of many fishermen to navigate are two of the more important.

Of interest is the fact that a predominant part of the pelagic fish catch is consumed fresh, dried, or processed into various fish pastes. This is even true of the clupeoids, which in other parts of the world are either canned or reduced to fish meal.

HYDROGRAPHY

In the western North Pacific, the dominant feature in the current system is the Kuroshio. Upstream of the Kuroshio, the North Equatorial Current moves westerly north of about lat. 5^{o}N. To the east of the Philippines, the North Equatorial Current separates into two branches. The northern branch moves northward along the Philippine Islands and Taiwan, where it becomes the Kuroshio. The southern branch forms the eastward flowing Equatorial Countercurrent. After passing Taiwan, the Kuroshio flows in a northeasterly direction through the Ryukyu Islands. At the northern sector of the Ryukyu chain, the Kuroshio sends off a branch northward as the Tsushima Current, which provides warm equatorial waters to the Sea of Japan and to parts of the East China Sea and the Yellow Sea. The main core of the Kuroshio flows along the east coast of Japan, and under average conditions, turns eastward at about lat. 35°N and becomes known as the Kuroshio Extension Current.

For much of the tropical and southwestern Pacific areas, the current pattern is dominated by the monsoons. Wyrtki (1961) provides an excellent review of the general circulatory pattern prevailing in the southwest Pacific. At the height of the northern monsoon in February the high pressure system is fully developed over the Asiatic Continent. The prevailing winds are northeasterly north of the Equator and northerly at the Equator. In the southern latitudes, between the Equator and lat. 10°S, the winds are northwesterly, but south of lat. 19°S they are southeasterly. The flow of the surface ocean currents shows a similar pattern to the winds. Figure 2 shows the general flow of the surface currents in February.

At the height of the southern monsoon in August, the South Equatorial Current is fully developed. Pacific water moves into southeast Asia south of Mindanao and south of Halmahera Island (Fig. 3). The current flow is northwesterly along the northern coast of New Guinea and forms the principal source for the Equatorial Countercurrent.

JACKS, MULLETS, ETC.

This group includes a wide variety of species ranging from estuarine species such as the mullets (family Mugillidae) to the truly pelagic species such as the dolphin (family Coryphaenidae) and the saury (*Cololabis saira*).

The regional catch of fish in this category in 1963 was estimated at 1,003.7 thousand metric tons (Table III), which represents about 51 percent of the total world catch of 1,960.0 thousand metric tons. The actual landings of this group would be significantly larger than listed, since statistics are not available from a number of the major countries which undoubtedly utilize fish in this group, e.g., mainland China, Indonesia. Furthermore, since species such as scads and mullets can be taken by simple fishing gear, the amount caught and not reported by the many subsistence fisheries located throughout the area could be substantial.

Principal Species

Jack Mackerel

Trachurus japonicus (Japan, Korea)
Trachurus declivis (Australia)

Round Scad

Decapterus macrosoma (Philippines)
Decapterus russelli (Philippines)

Saury

Cololabis saira (Japan, Korea)

Landings by Country

Table IV shows the 1968 landings of the principal species listed above. The jack mackerel (*T. japonicus*) landings in Japan reached a post World War II peak of 595.7 thousand metric tons in 1960 (Japan, Ministry of Agriculture and Forestry, 1963). The most dramatic increase occurred in 1952 when the total landings increased from 92.6 thousand metric tons in 1951 to 206.3 thousand metric tons. Other species of jack mackerel are caught also throughout the area but the catches are not large.

The fishery for round scads (*D. macrosoma* and *D. russelli*) has developed into the most important fishery in the Philippines where the bulk of the western Pacific catches are landed. In 1956 the total catch was estimated to be 19.0 thousand metric tons; there has been a rapid increase in landings since 1965 and in recent years the annual catch has exceeded 150.0 thousand metric tons. The maximum catch to date was the 206.8 thousand metric tons landed in 1967.

The landings of saury (*C. saira*) have undergone considerable fluctuations. Japan, the leading producer of saury, increased its catches in the 1950's and recorded a high of 575.1 thousand metric tons in 1958 (Japan, Ministry of Agriculture and Forestry, 1963). Since then there has been a general decline in catches, and in 1969 Japan's total saury catch was about 51.0 thousand metric tons (Japan, Ministry of Agriculture and Forestry, 1970).

Method of Fishing

The principal gear used to catch jack mackerel is the purse seine; however, hand lines are also used throughout the area. In the round scad fishery in the Philippines a specialized bag net method of fishing, developed in the post World War II years, is used (Tiews, Ronquillo and Caces-Borja, 1970). In recent years purse seining also become more popular. The purse seine nets used are 250-270 fathoms long, 45 fathoms deep, and are hauled in by power blocks. The development of this gear was chiefly responsible for the dramatic increase in landings of this species. Fishing is done at night with the aid of lights to attract the fish.

The saury fishery also utilizes a net and light system as the principal method of capture. This method, called the "stick-held dip net", depends on the strong phototaxic response of saury. Drift nets are used also to catch saury in commercial quantities.

Biology and Stock Assessment

Jack mackerel are found throughout the IPFC and quite a bit of the life history of this species is known. On the Pacific side *T. japonicus* is known to move northward from the southern waters to the north end of Honshu Island. These fish remain in the Honshu area until November when they begin the return movement to the south. In the Sea of Japan this species is known to move from south of Kyushu Island to near the northern end of Honshu Island. Spawning occurs from March to July (Fukataki, 1960).

Unlike the stocks of jack mackerel in northern waters, which are fished commercially, the stocks of jack mackerel in the Southern Hemisphere are virtually untouched. The southern species, *T. declivis,* occur on the Continental Shelf of Southern Australia, from Shark Bay, Western Australia to Newcastle, New South Wales, and around the coastal waters of Tasmania and New Zealand (Fraser and Hynd, 1967). The potential yield of this species has been estimated by CSIRO to be of the order of 100.0 thousand metric tons (Gulland, in press). Information of the life history and biology of *T. declivis* is fragmentary.

The distribution of round scad (*Decepterus spp.*) is probably similar to that of the jack mackerel. In the Philippines the round scad fishery depends upon two species, *D. macrosoma* and *D. russelli.*

Although studies of the round scad in Philippine waters have been made recently (Tiews, Ronquillo and Caces-Borja, 1970; Ronquillo, 1970), much of the biology and population dynamics of the two principal species are still unknown. The fishery is centered in the Sulu Sea area and is based mainly on

2-year-old fish (Ronquillo, 1970). While estimates of the size of the resour are not available, an expansion of this fishery in the Philippines is believe possible (Tiews, Ronquillo and Caces-Borja, 1970).

A considerable amount of information is available on the biology of th saury in the North Pacific. The appearance of saury in abundance off Japan varies with locality; off Hokkaido from August-October and off Honshu from September-December. The saury moves shoreward and southward with the onset of winter.

Presently a fishery does not exist for saury in the Southern Hemispher but information being accumulated indicate that a sizable resource may exist in the South Pacific (information provided by A. Suda).

HERRINGS, SARDINES, ANCHOVIES, ETC.

The clupeoids and related species form the most important (by weight) group of fishes taken commercially in the world. In 1968 the world catch of clupeoids was 20,460.0 thousand metric tons, constituting about 32 percent of the world's total fish catch.

Principal Species

Sardines

Sardinops melanosticta (Japan, Korea)
Sardinops neopilchardus (Australia)
Sardinella perforata (Philippines)
Sardinella fimbriata (Philippines)
Sardinella sirm (Philippines)
Sardinella longiceps (Philippines)
Clupea (Harengula) longiceps (Indonesia)
Other species and genera elsewhere

Anchovies

Engraulis japonicus (Japan)
Other species and genera elsewhere

Landings by Country

Table III provides estimates of the marine clupeoid landed in 1968 by countries in the western Pacific area. The total catch of 767.5 thousand metric tons represents about 4 percent of the world's total catch of this group. Only a small fraction of the catch was made in southern waters; Japan was the largest producer with 527.0 thousand metric tons. In the Philippines the sardines and the anchovies are the second and third most important fishes taken commercially.

Method of Fishing

The fishing gear used for catching marine clupeoids varies from the simple dip net to sophisticated purse seines fished from powered vessels (Li, 1960; von Brandt, 1960). In Japan the enveloping nets account for about 58 percent of the total sardine catch, whereas the gill nets take an additional 29 percent (von Brandt, 1960). In the Philippines approximately 90 percent of the total marine clupeiod catch is made with bag nets.

Biology and Stock Assessment

The distribution of the various species of marine clupeoids follows the pattern of other organisms; the number of species increases from the higher to lower latitudes (Longhurst, MS*). Published records show the diversity of species within this group. Thirty-three species of clupeoids have been reported from Taiwan waters, (Yuan, 1970) whereas Ronquillo (1960) reported nine species of *Sardinella* in Philippine waters.

One of the most important aspects of marine clupeoids is the tremendous fluctuations in landings that a number of species has undergone in different parts of the world (e.g., California and Japan, Longhurst MS*). The landings of sardines, principally *S. melanosticta,* has declined dramatically in Japan. From 1925 to 1938 the average annual landing of sardines in Japan was 1,550.0 thousand metric tons (Tokai Regional Fisheries Research Laboratory, 1960); since 1945 the total annual landings have been at very low levels, varying from 200.0 to 500.0 thousand metric tons. The decline has been attributed not to over-fishing, but to environmental changes that had led to reduced recruitment (Nakai, 1960). Interestingly, during the period of abundance the major proportion of the catch came from the Pacific east of Japan. In the period of low catches the major center of abundance was in the Sea of Japan.

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* Longhurst, A. (MS). The clupeoid resources of the tropical seas. National Marine Fisheries Service, Fishery-Oceanography Center, La Jolla, California.

The virtual collapse of the sardine fishery in Japan stimulated considerable research in this species. Consequently, of the commercially important fish species taken in Japan the biology of the sardine is probably the best known and documented.

S. melanosticta is reported to move northward in the spring from south of Kyushu Island and southward in autumn along both coasts of Japan and also off Korea. The fishing season varies with locality; off southern Kyushu Island the season extends from December to March while off central Honshu the season is from March to early June. Spawning occurs in the Sea of Japan and extends from January to May.

The biology of the anchovy (*E. japonicus*) found off Japan is better known than the other species of anchovies found elsewhere in the western Pacific. *E. japonicus* occurs in Japanese coastal waters all year round. Spawning is reported to take place at the edge of the Continental Shelf. Lim and Lee (1970) reported that 96 percent of all fish eggs and 77 percent of all fish larvae taken in plankton net tows in Korean waters were of *E. Japonicus*. South of Japan anchovy species of the genus *Stolephorus* appears to be the most important (Tiews, Ronquillo and Santos, 1970).

Since marine clupeoids occupy the lower end of the food web, their occurrence in large numbers is related to areas of upwelling, e.g., the tremendous anchovy resource in waters off Peru is associated with intense upwelling there. Because the waters in the northern sector have been intensively surveyed, it is unlikely that new resources of marine clupeoids will be uncovered there. The same cannot be said about the southern sectors because the areas of upwelling have not been adequately surveyed with respect to both the intensity and extent of upwelling and the presence of clupeoids. Areas deserving attention include the Banda Sea (Wyrtki, 1961), the coasts of Indonesia, Sarawak, and Makassar (Shomura and Gulland, in press) where some upwelling occurs.

The potential yield of marine clupeoids along the coast of Australia has been estimated to exceed 100.0 thousand metric tons Gulland (in press). Blackburn (1960) reported aerial sightings of 10,000 schools of *S. neopilchardus* in 1 day off the south coast of western Australia. Considering that the Australian catch of clupeoids in 1968 was 0.8 thousand metric ton, the resource can certainly be judged as underutilized.

TUNAS, BONITOS AND SKIPJACKS

Among the pelagic fishes the tunas represent the most difficult group in terms of pinpointing location of capture. The fisheries for tunas are truly distant-water fisheries and many nations fish great distances from their home ports for the various species of tuna.

Principal Species

Thunnus alalunga (albacore, widespread distribution)
Thunnus albacares (yellowfish tuna, widespread distribution)
Thunnus maccoyii (southern bluefin tuna, Australia and New Zealand)
Thunnus obesus (bigeye tuna, widespread distribution)
Thunnus thynnus (bluefin tuna, Japan, Korea, Taiwan)
Katsuwonus pelamis (skipjack tuna, widespread distribution)

Landings by Country

Table III lists the 1968 catch of tunas, bonitos, and skipjacks for the countries located in the western Pacific. Since the tuna fisheries of Japan, Korea and Taiwan range throughout the world's oceans, an estimate has been made of the total catch from the area south of lat. 30°N (Table V).

Method of Fishing

The method of fishing for tunas varies with the locality and the species sought. In northern latitudes the albacore and skipjack tuna are taken primarily by the pole-and-line technique using live bait (Van Campen, 1960; Isa, 1970). Albacore are taken also on longline gear. Bluefin tuna in northern waters are taken on longline gear and in set nets in Japanese coastal waters. In tropical waters the longline is the principal gear used to catch yellowfin tuna and bigeye tuna. Other gear such as trolling and hand line are used for catching tunas in the subsistence fisheries throughout the area.

The pole-and-line method using live bait is presently the principal method of fishing for skipjack tuna in the western Pacific; however, Japan and the United States are testing the feasibility of using purse seine to catch skipjack tuna in commercial quantities (Miller, 1970).

In the higher latitudes of the Southern Hemisphere, especially around New Zealand and Australia, the longline gear is used to take southern bluefin tuna. Attempts to catch this species there in commercial quantities with the pole-and-line technique were unsuccessful (Hynd and Vaux, 1963).

Biology and Stock Assessment

A wealth of information on the biology of various species of tunas of the western Pacific is available in the literature (see for example, papers presented at the FAO World Tuna Conference (Rosa, 1963-64) and the State of Hawaii Governor's Conference (Manar, 1966). Perhaps the most important areas which need further attention are stock identification and stock assessment. Regarding stock identification, tagging experiments have demonstrated the transpacific movements of bluefin tuna and albacore (Clemens and Flittner, 1969, Clemens, 1961, Otsu, 1960; Otsu and Uchida, 1963) and the movement of skipjack tuna in Trust Territory waters (Otsu, 1970), but more intensive work is needed, especially in waters within the East Indies Archipelago.

Regarding stock assessment studies, Rothschild and Uchida (1968) indicated that an increase in effort of the longline fishery for albacore, yellowfin tuna, and bigeye tuna would not result in any substantial increase in catch. Precise estimates of the potential increase in the yield of skipjack tuna are not available; however, some evidence suggests that the increase in the central Pacific may be substantial (Rothschild, 1966; Silliman, 1966). For the western Pacific, Gulland (in press) estimated the potential yield of skipjack tuna to be in the order of 250.0 thousand metric tons.

There has been considerable concern in recent years regarding the stock size of the southern bluefin tuna in waters around Australia and New Zealand. The longline fishing vessels of Japan, which landed from 10 to 20 tons of southern bluefin tuna per day 7 or 8 years ago are presently averaging less than 1 ton per day (Suisan Keisai Shinbun, 1970).

MACKERELS, BILLFISHES, CUTLASSFISHES, ETC.

Among the several groups of species listed in this general category, the mackerels, principally species of the genera *Scomber, Rastrelliger* and *Scomberomorus* are the most important in terms of landings and value. Table III provides a summary of the total catch of this group by country for 1968.

Principal Species

Scomber japonicus (Japan, Korea, Taiwan)
Scomber tapeinocephalus (Japan, Korea, Taiwan)
Rastrelliger neglectus (widespread throughout southeast Asia)
Rastrelliger kanagurta (widespread through southeast Asia

Landings by Country

Table VI lists by country the 1968 catch of the various species of mackerel. Of the two species of *Scomber (S. japonicus* and *S. tapeinocephalus)* present in northern latitudes, *S. japonicus* is by far the predominant species in the commercial catch of Japan and *S. tapeinocephalus* in the catch of Taiwan (Yuan, 1970). Pathansali (1967) reported that up to 50 percent of the catch listed as *Rastrelliger* in Malaysia may be that of a *Scomber* species. An unidentified species of *Scomber* also is reported to be present in commercial catches in the Philippines.

The major fisheries for *Rastrelliger* in the western Pacific are in Thailand and Malaysia.

Method of Fishing

The purse seine is the principal commercial gear for catching *Scomber* and *Rastrelliger*. Other commonly used gear include hand line, gill net, lift net with light seine, beach seine, and fish corral (Yuan, 1970).

Biology and Stock Assessment

Although some problems in systematics still remain, e.g., *Scomber* vs. *Pneumatophorus* as the generic term and identification problems in Malaysia (Pathansali, 1967), a considerable amount of information is available on the biology of this group, especially for those species occurring off Japan and Korea. Tagging studies in the Sea of Japan show a northward migration of *S. japonicus* in summer and a southward movement in late fall (Machinaka, 1960). With regard to the population structure Kawasaki (1969) suggests that there are three populations of *S. japonicus* in the seas around Japan.

The fishery for mackerel *(Scomber spp.)* in Japan has shown a phenomenal growth in recent years. From an average annual landing of 242.9 thousand metric tons for the period 1951-55 (Japan, Ministry of Agriculture and Forestry, 1963), the catch has increased to 1,015.0 thousand metric tons in 1968. This marked increase in landings by the Japanease fishery has been attributed to an increase in abundance, rather than being entirely due to expansion of fishing area and increase in fishing effort. Scientists believe that there has been a shift in the spawning grounds of the mackerel, as a result of major changes in environmental conditions. It is believed that changes in the environment have led to better survival of the young, thus resulting in an increase in population.

Thailand has carried out over the past several years a concerned study of the *Rastrelliger* group. A recent study of the catch and effort data obtained from the commercial fishery in Thailand has led to a preliminary assessment of the stock size (Kurogane et al MS*). On the basis of this study, it is believed that the Thailand fishery for *Rastrelliger* is presently operating at an optimal level. It was estimated that a two fold increase in fishing intensity now would result in an increase in yield of only 20 percent accompanied by a decrease in catch per unit of effort of 40 percent.

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TABLE I

Annual fish landings by western Pacific countries

Country	Year	Fresh water and diadromous fishes	Marine		Unsorted and unidentified	Others	Total
			Demersal[1]	Pelagic[2]			
		Thousand metric tons					
Australia	1968	0.7	18.6	26.8	1.6	55.0	102.7
China (mainland)	1960[3]	4,000.0			(1,800.0)		5,800.0
China (Taiwan)	1968	37.6	92.5	255.1	81.2	60.9	527.3
Hong Kong	1968	30.1	30.3	19.6	17.7	3.4	101.1
Indonesia	1969[4]	447.0			(762.4)		1,209.4
Japan	1968	230.4	2,540.0	2,897.8	776.4	2,225.2	8,669.8
Korea (North)	1957[3]						291.0
Korea (Republic)	1968	6.2	155.1	208.1	141.7	330.0	841.1
Malaysia (excludes Sarawak)	1968	29.2	42.2	190.6	73.2	71.3	406.5
New Zealand	1967	0.2	29.0	6.7	0.3	23.4	59.6
Philippines	1968	153.3	238.7	493.6	5.3	53.7	944.6
Singapore							20.0
Ryukyu Islands	1968[5]	-	1.7	22.8	8.9	1.5	34.9
Thailand	1968	81.1		160.4	602.3	245.0	1,088.8
Vietnam (North)	1962[3]						289.0
Vietnam (Republic)	1969[7]	63.7			(355.5)	44.7	463.9
Total							20,849.7

[1] Includes landings of fishes listed in the Yearbook of Fishery Statistics (FAO, 1969) as (1) flounders, halibuts, soles, etc. and (2) redfishes, basses, congers, etc.

[2] Includes landings of fishes listed in the Yearbook of Fishery Statistics (FAO, 1969) as (1) jacks, mullets, etc., (2) herrings, sardines, anchovies, etc., (3) tunas, bonitos, skipjack, (4) mackerels, billfishes, cutlassfishes, etc., and (5) sharks, rays, chimaeras.

[3] Shomura and Gulland (in press).

[4] U.S, Bureau of Commercial Fisheries, 1970.

[5] Estimate provided by Dr. Tham Ah Kow, University of Singapore, Singapore.

[6] Demersal catch probably listed in "unsorted and unidentified" category.

[7] Brouillard, 1970.

TABLE II

Average annual rates of growth of fisheries production 1960-67 (from Comitini, 1970 : Table 2)

Country	Growth rates
Thailand	26.0[1]
West Malaysia	11.6[1]
Indonesia	8.3[1]
Philippines	7.7
Taiwan	8.5
Japan	3.5[2]
Korea	11.8

[1] Marine production only.

[2] Excludes whaling.

Sources : Thailand, Statistical Section, Department of Fisheries, Bangkok.

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TABLE III

Landings of coastal and offshore pelagic fishes, 1968
(data from FAO, 1969)

Country	Jacks, mullets, etc.	Herrings, sardines, anchovies, etc.	Tunas, bonitos, skipjacks	Mackerels, billfishes, cutlassfishes, etc.	Sharks, rays, chimaeras	Total
						Coastal and pelagic fishes
		Thousand metric tons				
Australia	7.7	0.8	6.8	5.4	6.1	26.8
China (mainland			(No data)			
China (Taiwan)	34.0	30.0	101.8	56.2	33.1	255.1
Hong Kong	10.6	3.8	-	3.0	2.2	19.6
Indonesia			(No data)			
Japan	607.3	527.0	545.0	1,165.0	53.0	2,897.8
Korea (North)			(No data)			
Korea (Republic)	44.3	68.0	43.6	34.2	18.0	208.1
Malaysia (excludes Sarawak)	35.2	38.3	5.2	104.9	6.5	190.6
New Zealand[1]	4.5	-	-	0.2	2.0	6.7
Philippines	258.9	99.1	44.5	90.0	1.1	493.6
Singapore			(No data)			
Ryukyu Islands	0.7	-	19.1	2.0	1.0	22.8
Thailand	-	-	-	148.1	12.3	160.4
Vietnam (North)			(No data)			
Vietnam (Republic)			(No data)			
Total	1,003.7	767.5	766.0	1,609.0	135.3	4,281.5

[1] Landings for 1967.

TABLE IV

Landings of the principal species in the "jacks, mullets, etc." category, 1968 (data from FAO, 1969)

Country	Horse mackerel, jack mackerel, scad	Saury
	Catch in thousand metric tons	
Japan	358.0	140.0
Philippines	160.6	
China (Taiwan)	16.7	
Malaysia (West Malaysia)	6.9	
Hong Kong	5.1	
Korea (Republic)	2.5	29.9
Ryukyu Islands	0.3	

TABLE V

Average landings of tunas and related species, 1965-67 (data provided by A. Suda)

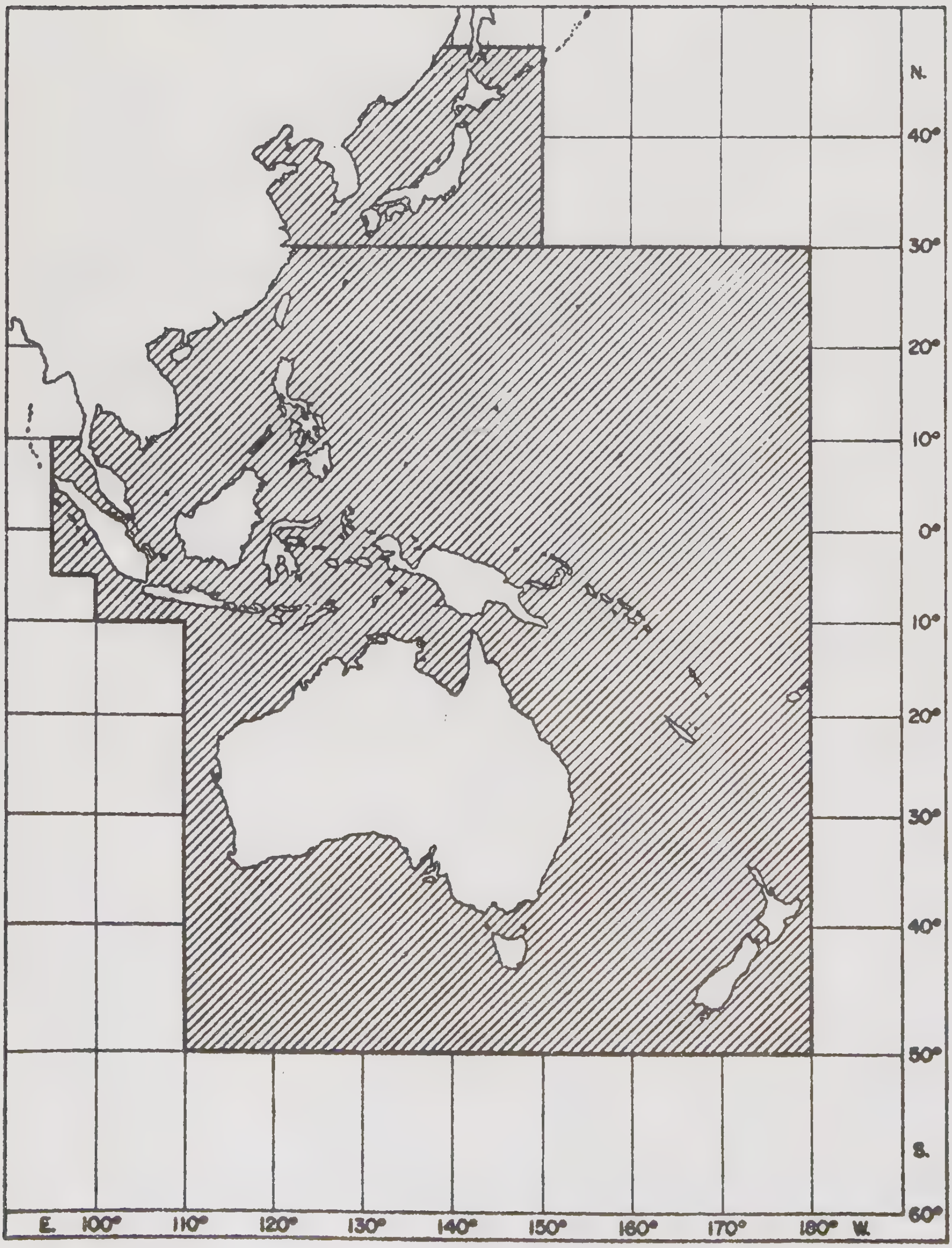
Country	Catch
	Thousand metric tons
Japan	182.0
Korea (Republic)[1]	7.5
Ryukyu Islands	6.6
Taiwan[1]	15.9
Malaysia	5.0
Philippines	27.0
Australia	7.0
New Hebrides	3.4

[1] Fifty percent of the catch of each country from the Pacific and Indian Oceans is allocated to the IPFC areas.

TABLE VI

Landings of mackerel, 1968

Country	Mackerels (*Scomber* spp., *Pneumatophorus* spp.)	Indian mackerel (*Rastrelliger* spp.)	Spanish mackerel, seer-fishes (*Scomberomorus* spp., *Cybium* spp.)
Australia	-	-	1.0
China (mainland)		(No data)	
China (Taiwan)	19.0	-	4.1
Hong Kong	1.5	-	-
Indonesia		(No data)	
Japan	1,015.0	-	20.0
Korea (North)		(No data)	
Korea (Republic)	10.5	-	5.1
Malaysia (excludes Sarawak)	-	95.6	6.9
New Zealand	-	-	-
Philippines	-	49.9	9.8
Singapore		(No data)	
Ryukyu Islands	-	-	-
Thailand	-	148.1	-
Vietnam (North)		(No data)	
Vietnam (Republic)		(No data)	


N.
40°
30°
20°
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0°
10°
20°
30°
40°
50°
S.
60°
E.
100°
110°
120°
130°
140°
150°
160°
170°
180°
W.

Fig. 1. Area included in the discussion of coastal and high-seas pelagic resources.

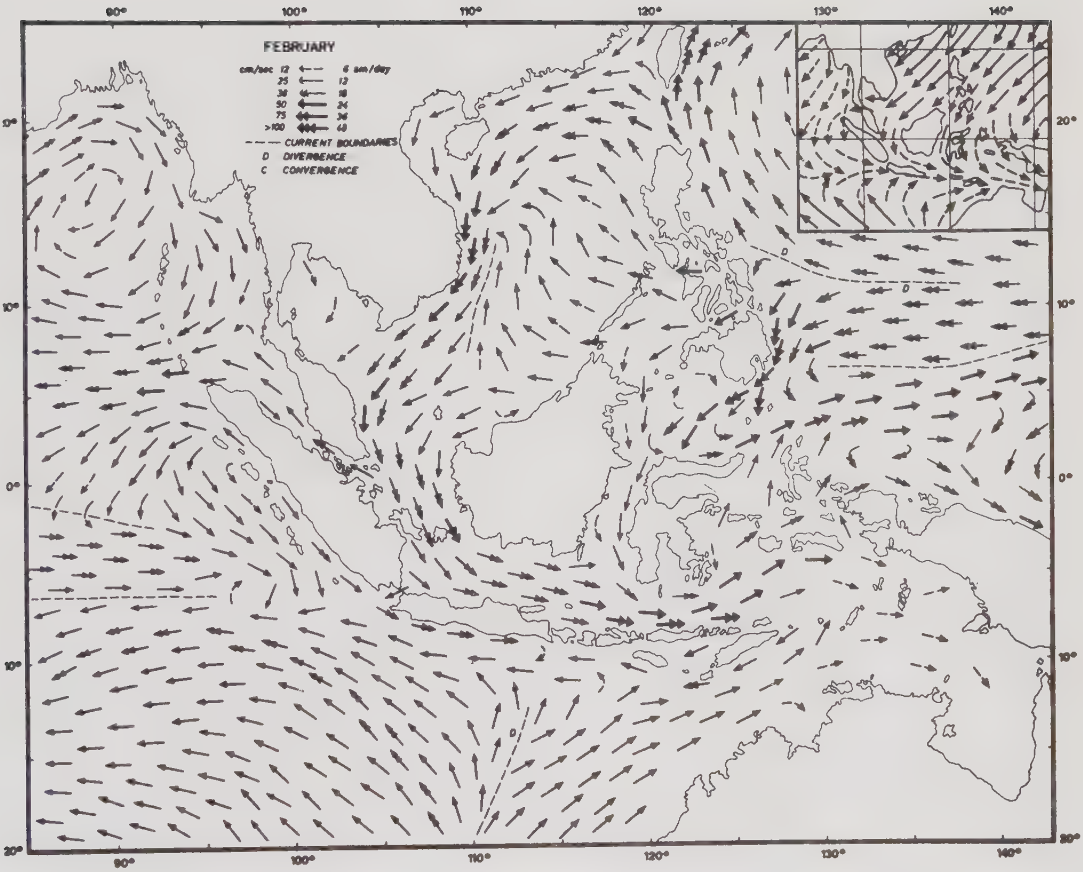
FEBRUARY
cm/sec 12 6 sm/day
25 12
38 18
50 24
75 36
>100 48
CURRENT BOUNDARIES
D DIVERGENCE
C CONVERGENCE
90°
100°
110°
120°
130°
140°
20°
10°
0°
10°
20°

Fig. 2. General circulation of surface water in February (from Wyrtki, 1961).

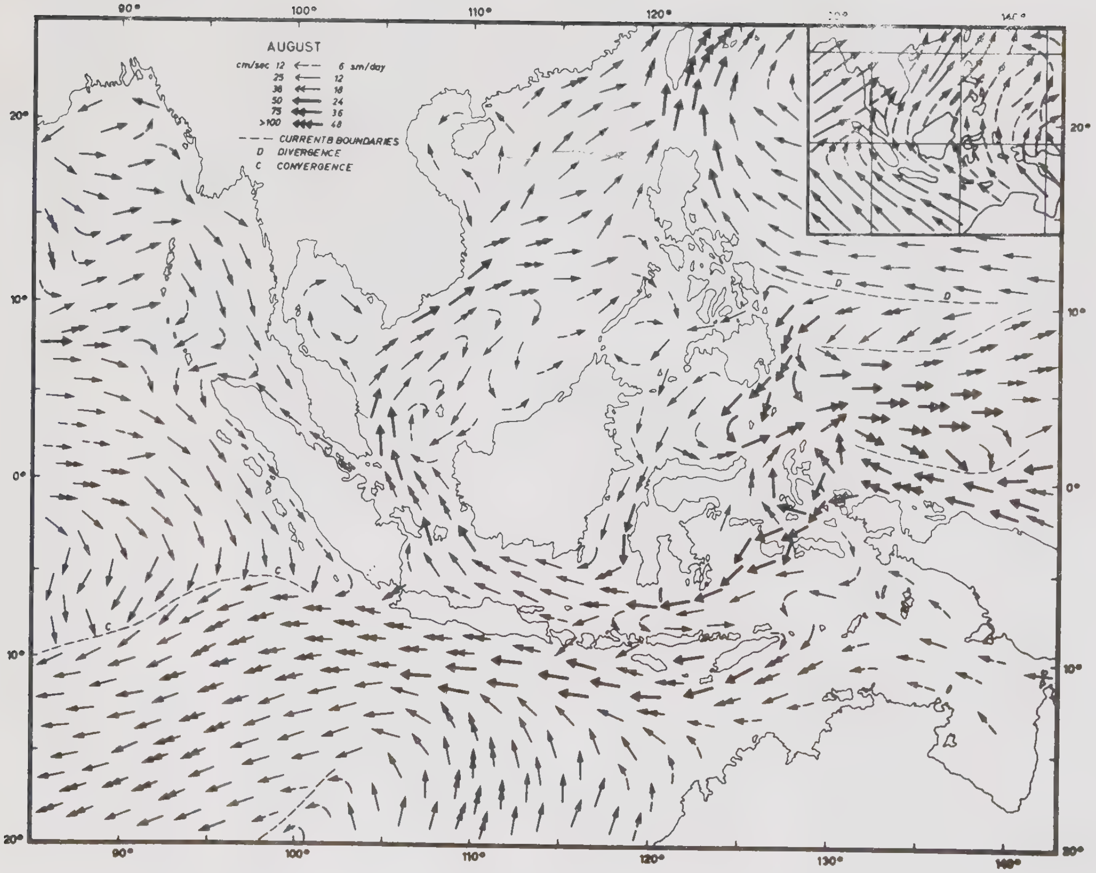
AUGUST
cm/sec 12 6 sm/day
25 12
38 18
50 24
75 36
>100 48
CURRENTB BOUNDARIES
D DIVERGENCE
C CONVERGENCE
90°
100°
110°
120°
130°
140°
20°
10°
0°
10°
20°
D
D
C
C

Fig. 3. General circulation of surface water in August (from Wyrtki, 1961).

7148

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An Annotated List of Protozoan Parasites, Hyperparasites, and Commensals of Decapod Crustacea*

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SYNOPSIS. An approximately complete list of the known protozoan associates (exclusive of a few aberrant forms like *Amallocystis*) of decapods is presented. A few taxonomic changes are suggested. Host, site of infection and geographic location are mentioned. Some comments on pathogenicity are made.

THIS is principally a taxonomic paper, intended to present in a systematic manner a complete list of the protozoa known to be associated with decapods and to deal with a few of the problems in classification and nomenclature found at the generic and specific levels. At the same time, such highly relevant matters as host and site of infection, locality and pathogenicity are mentioned.

At the higher levels of classification we followed "A revised classification of the phylum Protozoa" of the Honigberg Committee (78) as far as we could but were unable to follow it consistently because several specialists consider different parts of that system inadequate. In classifying the Amoebae we have followed Bovee and Jahn (20). Commenting on their difficulties, they stated very clearly the nature of some of the basic problems: "One reason these families are difficult to deal with is the consensus of taxonomists of protozoa (Honigberg et al., 1964) which still fails to recognize fully that protozoa are at least as evolutionally ancient and taxonomically diverse as are the metazoa. The protozoa probably should be considered at least a subkingdom (or kingdom) of organisms, containing several phyla and subphyla (Raabe, 1964). This idea was well presented by Raabe, and was discussed at length and strongly emphasized by Kozloff (1960) in a symposial address; and kingdoms were suggested—but not adopted—by Corliss (1962)." In the classification of the "sporozoa" we have followed Levine (128), who has given the most recent modification. However, the comment just quoted from Bovee and Jahn is applicable also to this, because the "Sporozoa" probably include at least 3 distinct phyla. We have followed the Honigberg Committee on classification of the ciliates, since that part, strongly influenced by the opinions of Corliss, has not been so controversial.

Altho we have listed most of the protozoa reported as associates of decapods, these are doubtless a small fraction of those which actually occur. Probably all decapods harbor protozoan parasites; few species are known because relatively few decapods have been examined.

The pathogenicity of protozoan infections in decapods is poorly understood but a few general statements may be made. The one known amoeba is highly pathogenic to its crab host. Gregarines do not seem to be very pathogenic, altho they cause some local damage and occlude passages in the inhabited organ (9) with serious results. Microsporida are notorious pathogens and generally kill the decapod host. A few ciliates are pathogenic in decapods but many are harmless commensals.

Even when we can state with confidence that a parasite is or is not particularly pathogenic to a decapod host, we know little about what this means in terms of the fluctuation of the host populations.

Subphylum SARCOMASTOGOPHORA Honigberg & Balamuth, 1963 (78).

Superclass SARCODINA Hertwig & Lesser, 1874 (78).
Class HYDRAULEA Jahn & Bovee, 1965 (85).
Order HYALOPODIA Bovee & Jahn, 1966 (20).
Family PARAMOEBIDAE Poche, 1913 (153).
Genus *Paramoeba* Schaudinn, 1896 (169).

Paramoeba perniciosa Sprague, Beckett & Sawyer, 1969 (190). Syn.: *Paramoeba* sp. Sprague & Beckett, 1968 (185). In hemolymph of blue crab *Callinectes sapidus* Rathbun, 1896. Chincoteague Bay, Virginia and Maryland, USA (165, 166, 167, 184, 185, 190); coast of North Carolina and Georgia, USA (129). Dr. Eugene E. Bovee (pers. com.) thinks *P. eilhardi* Schaudinn, 1896, the type species, belongs to genus *Mayorella* and (in press) has rejected both genus *Paramoeba* Schaudinn and family Paramoebidae Poche. If Bovee's opinion is justified, which we see no reason to doubt, then *P. perniciosa* must be transferred to another genus. Since we hold no opinion as to the correct systematic position of this amoeba we have, for convenience, used the old classification here.

Subphylum APICOMPLEXA Levine, 1970 (128).

Class SPOROZOEA Leuckart, 1879 (128).
Subclass GREGARINIA Dufour, 1828 (78).
Order EUGREGARINIDA Léger, 1900 (78).
Family CEPHALOIDOPHORIDAE Kamm, 1922 (90).
Genus *Cephaloidophora* Mavrodiadi, 1908 (90).

Cephaloidophora bermudensis (Ball, 1951) n. comb. Syn.: *Carcinoecetes bermudensis* Ball, 1951 (10). In mid- and hindgut of the grapsid crab *Pachygrapsus transversus* (Gibbs). Bermuda. The generic name *Carcinoecetes* Ball, 1938 (7), is a junior synonym of *Nematopsis* (210). The present species does not seem to have any of the essential characters of *Nematopsis* but is much like *Cephaloidophora*, to which genus it is here provisionally transferred.

Cephaloidophora carpilodei Ball, 1963 (13). In the gut of the xanthid crab *Carpilodes rugatus*. Cocoanut Island, Hawaii, USA.

Cephaloidophora conformis (Diesing, 1951) Léger & Duboscq, 1911 (122). Syns.: *Gregarina conformis* Diesing, 1851 (90); *Aggregata conformis* (Diesing, 1851) Labbé, 1899 (107); *Frenzelina conformis* (Diesing, 1851) Léger & Duboscq, 1907 (116); *Carcinoecetes conformis* (Diesing, 1851) Ball, 1938 (7). In the ceca the gut lumen of the grapsid crab *Pachygrapsus marmoratus* Fabricius. Mediterranean coast of France; coast of Tunisia (214); northeast coast of Spain (213). Tuzet and Ormières (210) declared the name *Carcinoecetes* Ball, 1938, a junior synonym of *Nematopsis* Schneider and returned this species to genus *Cephaloidophora.*

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Cephaloidophora drachi Théodoridès, 1962 (201). Syn.: *Cephaloidophora* sp. Tuzet & Ormières, 1961 (210). In the gastric ceca of the xanthid crab *Xantho rivulosus* (Risso). Banyuls, France.

Cephaloidophora dromiae (Frenzel, 1885) Vivarès & Rubió, 1969 (213). Syn.: *Gregarina dromiae* Frenzel, 1885 (61). In gut of the crab *Dromia personata* (= *vulgaris*) (61, 214). Gulf of Naples (61), Blanes, Spain (213); and coast of Tunisia (214). Altho Théodoridès (201) suggested that this gregarine probably should be placed in genus *Cephaloidophora*, the new combination is here attributed to Vivarès and Rubió (213), who first used it.

Cephaloidophora duboscqi Poisson, 1924 (154). In the gut of the alpheid shrimp *Athanas nitescens* Leach. Luc-sur-Mer (Calvados) (154) and Roscoff (211), France.

Cephaloidophora etisi (Ball, 1959) n. comb. Syn.: *Carcinoecetes etisi* Ball, 1959 (12). In the crab *Etisus laevimanus* Randall. Bombay, India. *Carcinoecetes* Ball, 1938, is a junior synonym of *Nematopsis* (210). The description of the present species fits that of *Cephaloidophora* rather than that of *Nematopsis.*

Cephaloidophora foresti Théodoridès, 1967 (205). In the gut of the crab *Xantho poressa* (Olivi). Banyuls and Villefranche, France.

Cephaloidophora fossor (Léger & Duboscq, 1907) Trégouboff, 1912 (208). Syns.: *Aggregata coelomica* Léger, 1901 [partim] (110); *Frenzelina fossor* Léger & Duboscq, 1907 (116). In gut of the pea crab *Pinnotheres pisum* Penn, living in *Mytilus edulis* L. France (English Channel) (110).

Cephaloidophora guinotae Théodoridès, 1967 (205). In gastric ceca of the xanthid crabs *Xantho granulocarpus* Forest (205), *Pilumnus hirtellus spinifer* Milne-Edwards (205, 213) and *P. hirtellus L.* (205). The 1st 2 hosts at Banyuls and the 3rd at Villefranche, France (205); the 2nd also at Blanes, Spain (213).

Cephaloidophora knoepffleri Théodoridès, 1962 (201). In gastric ceca of *Pinnotheres pinnotheres* (L.), a pea crab, commensal in the clam *Pinna nobilis* L. Banyuls, France (201); Blanes, Spain (213).

Cephaloidophora mithraxi (Ball, 1951) n. comb. Syn.: *Carcinoecetes mithraxi* Ball, 1951 (10). In the crab *Mithrax forceps* (Milne-Edwards). Bermuda. The generic name *Carcinoecetes* Ball, 1938 (7) is a junior synonym of *Nematopsis* (210). The present species does not resemble *Nematopsis* but its known characters are consistent with those of genus *Cephaloidophora* to which genus it is here transferred.

Cephaloidophora nephropis Tuzet & Ormières, 1961 (210). Syn.: *Porospora nephropis* Léger & Duboscq, 1915 [partim] (126). In the gut of the Norway lobster, *Nephrops norvegicus* (126, 127, 210, 212). Roscoff, France (126, 127, 210, 212).

Cephaloidophora nigrofusca (Watson, 1916) Kamm, 1922 (90). Syn.: *Frenzelina nigrofusca* Watson, 1916 (216). In gut of the fiddler crabs *Uca pugnax* and *U. pugilator.* Cold Spring Harbor, New York, USA.

Cephaloidophora ocellata (Léger & Duboscq, 1907) Kamm, 1922 (90). Syns.: *Aggregata vagans* Léger & Duboscq, 1903 [partim] (112, 116); *Frenzelina ocellata* Léger & Duboscq, 1907 (116). In gut lumen of the hermit crab *Eupagurus prideauxi* Leach. Banyuls, France (112, 201).

Cephaloidophora olivia (Watson, 1916) Kamm, 1922 (90). Syn.: *Frenzelina olivia* Watson, 1916 (216). In gut of 2 littoral crabs *Libinia dubia* Milne-Edwards (216) and *Ocypode cursor* L. (46). Cold Spring Harbor, New York, USA, (216) and Kalade, Lebanon (46).

Cephaloidophora pinguis Ball, 1963 (13). In gut of the xanthid crab *Carpilodes rugatus.* Cocoanut Island, Hawaii, USA.

Cephaloidophora poissoni Théodoridès, 1967 (205). In the alpheid shrimp *Alpheus ruber* Milne-Edwards and *A. dentipes* Guerin. Banyuls, France.

Cephaloidophora (?) *praemorsa* (Diesing, 1851) Kamm, 1922 (90). Syns.: *Gregarina praemorsa* Diesing, 1851 (90); *Aggregata praemorsa* (Diesing, 1851) Labbé, 1899 (107); *Frenzelina praemorsa* (Diesing, 1851) Léger & Duboscq, 1907 (116). In gut and vesicles adhering to the ovary of the crab *Cancer pagurus* L. As Kamm (90) pointed out, this nominal species is based on a mere reference by Redi, in 1684, to something which might have been a gregarine.

Cephaloidophora sp. Syn.: *Carcinoecetes* sp. Ball, 1948 (8). Mainly in the digestive gland but also in the gut lumen of the sand crab *Emerita analoga.* Southern California, USA. Since genus *Carcinoecetes* Ball, 1938 (7) is a junior synonym of *Nematopsis* Schneider, 1892 (210), this species needs to be reassigned. Most known gregarines of crabs belong either to genus *Cephaloidophora* or *Nematopsis.* The known characters of this species seems to be more like those of the former genus.

Genus *Cephalolobus* Kruse, 1959 (99).

Cephalolobus penaeus Kruse, 1959 (99). Attached to filter of stomach of shrimp *Penaeus aztecus* Ives and *P. duorarum* Burkenroad. Florida, USA. Type species. Kruse considered the systematic position of the genus in detail. He did not place it in a family but concluded, "If the life cycle of *C. penaeus* is proven to be similar to that of *Anisolobus*, both genera should be placed in a new family." Théodoridès (202), for reasons not very convincing assigned the genus to family Cephaloidophoridae, where it is here listed for convenience.

Cephalolobus petiti Théodoridès, 1964 (202). Active stages in stomach and cysts in hind-gut of the penaeid shrimp *Solenocera membranacea* (Risso). Banyuls, France.

Genus *Cardiohabitans* Ball, 1959 (12).

Cardiohabitans setnai Ball, 1959 (12). In the mid-gut of the shrimp *Penaeus semisulcatus* de Haan. Bombay, India. Type and only species. Ball did not assign the genus to a family but he compared it both with *Cephaloidophora* and genera in the Porosporidae; it is here provisionally listed with the Cephaloidophoridae. The validity of the genus is questionable.

Family URADIOPHORIDAE Grassé, 1953 (64).

Genus *Uradiofora* Mercier, 1912 (90).

Uradiophora athanasi Poisson, 1924 (154). In the gut of the alpheid shrimp *Athanas nitescens* Leach. Luc-sur-Mer (Calvados), France.

Uradiophora cuenoti (Mercier, 1911) Mercier, 1912 (90). Syn.: *Cephaloidophora cuenoti* Mercier, 1911 (90). In the gut of the shrimp *Atyaephyra desmaresti* Millet. Nancy, France.

Family POROSPORIDAE Labbé, 1899 (107).

Genus *Porospora* Schneider, 1875 (171).

Porospora gigantea (Beneden, 1869) Schneider, 1875 (171). Syn.: *Gregarina gigantea* Beneden, 1869 (17). In the lobster *Homarus gammarus* (L.) and the gastropod *Trochocochlea mutabilis* Philippi. Roscoff (171) and Banyuls (201), France. This is the type and the only species for which the essential generic character, naked sporozoites in a molluscan host, has been demonstrated. This demonstration was by a laboratory infection experiment performed by Hatt (72). The same author (71) obtained partial development also in *Mytilus minmus* Poli.

Porospora nephropis Léger & Duboscq, 1915, emend. Tuzet & Ormières, 1961 (210). Syn.: *Porospora nephropis* Léger & Duboscq, 1915 [partim] (126). In gut of the lobster *Nephrops norvegicus* L. Molluscan host unknown. Roscoff, France.

Porospora pisae Léger & Duboscq, 1911 (123). In the spider crabs *Pisa gibsii* (123) and *P. armata* (213). Cette (123) and Villefranche-sur-Mer (209), France; northeast coast of Spain

(213). Trégouboff (209) observed peculiarities in this species which convinced Léger and Duboscq (127) that it is not a *Porospora*. These authors did not attempt a reclassification for lack of information on final development of the cysts. Vivarès and Rubió concluded that it is neither a *Porospora* nor a *Nematopsis* (213). It is kept here in *Porospora* provisionally because there is still no clue as to its proper generic classification.

Porospora sp. Théodoridès & Laird, 1970 (206). In gut of the lobster *Homarus americanus*. St. Andrews, New Brunswick, Canada.

Genus *Nematopsis* Schneider, 1892 (172).

Nematopsis calappae (Ball, 1951) n. comb. Syn.: *Carcinoecetes calappae* Ball, 1951 (10). In gut of the oxystomatous crab *Calappa flammae* (Herbst). Intermediate host unknown. Bermuda. *Carcinoecetes* Ball, 1938, is a junior synonym of *Nematopsis* (210). Excepting rare intracellular stages, which could belong to another species, the known characters of this species are consistent with those of *Nematopsis*, to which genus this species is here provisionally assigned. It is noteworthy that Ball's figures show a porosporid character which the author did not mention, the "muscular collar" of the protomerite.

Nematopsis dorippe Bogolepova, 1953 (18). In gut of the oxystomatous crab *Dorippe granulata* de Haan. Sea of Japan.

Nematopsis duorari Kruse, 1966 (100, 101). In gut of the shrimp *Penaeus duorarum* Burkenroad. Spores in the pelecypods *Aequipecten irradians, Cardita floridana, Chione cancellata, Macrocallista nimbosa*. Florida, USA.

Nematopsis goneplaxi Tuzet & Ormières, 1961 (210). Syn.: *Porospora petiti* Théodoridès, 1962 (201). In gut of the crabs *Goneplax angulata* (Penn.) (210, 201) and *G. rhomboides* (213). Intermediate host unknown. Cette (210) and Banyuls (201), France; northeast coast of Spain (213).

Nematopsis grassei (Théodoridès, 1962) Vivarès & Rubió, 1969 (213). Syn.: *Porospora grassei* Théodoridès, 1962 (201). In gut of the oxystomatous crab *Calappa granulata* L. (201). Intermediate host unknown. Banyuls, France (201); northeast coast of Spain (213).

Nematopsis hesperus (Ball, 1938) Tuzet & Ormières, 1961 (210). Syns.: *Carcinoecetes hesperus* Ball, 1938 [TYPE SPECIES] (7); *Porospora hesperus* (Ball, 1938) Théodoridès, 1961 (200); [?] *Nematopsis* sp. Ball, 1951 (11). In gut of the grapsid crab *Pachygrapsus crassipes* Randall. Intermediate host unknown. California, USA.

Nematopsis legeri (de Beauchamp, 1910) Hatt, 1931 (73). Syns.: *Nematopsis mediterranen* Léger, 1905 [*nomen oblitum*] (113); *Porospora legeri* de Beauchamp, 1910 (16); *P. galloprovincialis* Léger & Duboscq, 1925 (127, 73). In gut of the crabs *Eriphia spinifrons* (16) and *E. verrucosa* (214); spores in the mussel *Mytilus galloprovincialis* and possibly other molluscs (73). Southern coast of France (16) and coast of Tunisia (214). This is one of the best known species of *Nematopsis*, due largely to the work of Hatt (70, 71, 73), who studied its entire life cycle by means of experimental infections. Previously only parts of the life cycle of a porosporid gregarine had been made known experimentally (124, 179). Tuzet and Ormières (210) recently made a careful study of this species to confirm the generic characters.

Nematopsis maraisi (Léger & Duboscq, 1911) Sprague, 1954 (179). Syn.: *Porospora maraisi* Léger & Duboscq, 1911 (123). In gut of the crabs *Macropipus* (= *Portunus*) *depurator* L. (123), *M. vernalis, Portumnus latipes* (214) and *Macropipus depurator* (213). Intermediate host unknown. Cette, France (123); coast of Tunisia (214); northeast coast of Spain (213).

Nematopsis matutae (Ball, 1959) Tuzet & Ormières, 1961 (210). Syn.: *Carcinoecetes matutae* Ball, 1959 (12). In gut of the crab *Matuta lunaris* (Forskål). Intermediate host unknown. Bombay, India.

Nematopsis mizoulei (Théodoridès, 1964) n. comb. Syn.: *Porospora mizoulei* Théodoridès, 1964 (202). In gut of the penaeid shrimp *Solenocera membranacea* (Risso). Intermediate host unknown. Banyuls, France. This species is transferred to genus *Nematopsis* because its vegetative stages are similar to those of confirmed species of this genus in crabs and shrimp but strikingly different from those of the single confirmed species of *Porospora*, known only in the lobster.

Nematopsis ostrearum Prytherch, 1938, emend. Sprague, 1949 (176). Syns.: *Nematopsis ostrearum* Prytherch, 1938 [partim] (159), *N. ostrearum* Prytherch, 1940 [partim] (160), [non] *N. legeri* (de Beauchamp, 1910): Kudo (103, 104). In gut of the xanthid crabs *Panopeus herbstii* Milne-Edwards (159, 160), *Eurypanopeus depressus* (Smith) (159, 160), *Neopanope texana sayi* (Smith) (97), *Eurytium limosum* (Say) (176, 180). Spores in the oyster *Crassostrea virginica* (Gmelin). Gulf and Atlantic coasts of North America, as far north as New York (109).

Nematopsis panopei Ball, 1951 (10). In the gut of the xanthid crabs *Panopeus occidentalis* Saussure and *P. herbstii* Milne-Edwards. Intermediate host unknown. Bermuda.

Nematopsis parapeneopsisi (Setna & Bhatia, 1934) n. comb. Syns.: *Hirmocystis* (?) *parapeneopsisi* Setna & Bhatia, 1934 (173); *Protomagalhensia* (?) *attenuata* Setna & Bhatia, 1934 (173). In gut of the shrimp *Parapeneopsis sculptilis* (Heller). Possible intermediate host unknown. Bombay, India. Grassé (64) concluded that these 2 species described by Setna and Bhatia were erroneously assigned as to genera. Altho mature cysts were not seen, the known characters (especially disappearance of septa in the satellites) of both species seem to be consistent with those of the Porosporidae. Furthermore, the difference between the 2 (slight difference in shape) seems to be insignificant. Thus, they are treated here as the same species. The specific name of that one appearing first in the paper is retained. Assignment is here made to genus *Nematopsis* because the known stages are much more like corresponding stages of this genus than those of *Porospora* and because the former (100) but not the latter is known to occur in shrimp. Théodoridès (202) suggested that these gregarines may belong to genus *Uradiophora* or maybe *Cephaloidophora*, but this suggestion is untenable because the septa of satellites do not disappear in these genera.

Nematopsis penaeus Sprague, 1954 (179). Syn.: *Porospora penaeus* (Sprague, 1954) Théodoridès, 1965 (203). In the gut of the shrimp *Penaeus aztecus* Ives. Intermediate host unknown. Barataria Bay, Louisiana, USA. Sprague (179) evidently mistook something else for intracellular stages of this parasite, for presence of these has not been confirmed. Kruse (99) reported this species in *P. aztecus, P. duorarum* and *P. setiferus*. Hutton et al. (79) found it in these and also *Sicyonia*. Later, Hutton (80) reported it in *P. aztecus, P. setiferus* (L.), *P. duorarum* Burkenroad, *P. brasiliensis* Latreil, *Sicyonia typica* Boeck, *Trachypenaeus similis* (Smith), *T. constricta* (Stimson), *Xiphopeneus krøyeri* (Heller) and *Solenocera atlantidis* Burkenroad. Considering that gregarines in these hosts have not been studied in detail, that Kruse found 2 species in 1 host, and that ecologic factors related to the different shrimp are diverse, it is probable that several species of *Nematopsis* in these shrimp have been mistaken for one. The work of Kruse (100, 101) supports Sprague's original generic determination.

Nematopsis portunidarum (Frenzel, 1885) Hatt, 1931 (73). Syns.: *Aggregata portunidarum* Frenzel, 1885 [partim] (61, 116, 127); *Nematopsis schneideri* Léger, 1903 (111, 127, 73); *Frenzelina portunidarum* (Frenzel, 1885) Léger & Duboscq, 1907 (116); *Porospora portunidarum* (Frenzel, 1885) Léger & Duboscq, 1911 (122). In gut of crabs *Carcinus maenas* (61, 122) and *C. mediterraneus* (214). Originally reported also in *Macropipus* (= *Portunus*) *arcuatus* (61) but Léger and Duboscq (122) reserved the specific name *portunidarum* for the gregarine in *Carcinus*. Develops experimentally in *Macropipus* (124, 125, 127). Spores in the molluscs *Cardium edule, Scrobularia plana* and perhaps others (127). Naples, Italy (61); Etang Pérols, near Montpellier, France (122); coast of Tunisia (214). Théodoridès (201, 203), apparently overlooking experimental proof by Léger & Duboscq (124, 125) that this is a *Nematopsis,* has continued to call it *Porospora. N. schneideri,* represented by spores in *Solen vagina,* is nominal type species by monotypy but, since this is regarded as a junior synonym of *N. portunidarum* (127, 73), the latter is now generally accepted as the type.

Nematopsis prytherchi Sprague, 1949 (176). Syns.: *Nematopsis ostrearum* Prytherch, 1938 [partim] (159); *N. ostrearum* Prytherch, 1940 [partim] (160). In the stone crab *Menippe mercenaria* (Say). Spores in the oyster *Crassostrea virginica* (Gmelin). Louisiana, Florida and the south Atlantic states of USA.

Nematopsis raouadi Vivarès, 1970 (214). In gut of the crab *Portumnus latipes.* Coast of Tunisia. It is curious that Vivarès, when comparing *N. raouadi* with *N. maraisi* in the same host, found gymnospores of the former to be the same size (3.8-4.5 μ) as that given by Léger and Duboscq (122) for the latter (4 μ), while finding the latter to be 7-8 μ.

Nematopsis soyeri (Théodoridès, 1965) n. comb. Syn.: *Porospora soyeri* Théodoridès, 1965 (203). In gut of the penaeid shrimp *Aristeus antennatus* (Risso). Intermediate host unknown. Banyuls, France. Desportes and Théodoridès (45) studied the ultrastructure of the gymnospores. This species is transferred to genus *Nematopsis* because its vegetative stages are similar to those of confirmed species of this genus in crabs and shrimp but strikingly different from those of the single confirmed species of *Porospora* known only in the lobster.

Nematopsis sp. Kruse, 1966 (100). In the gut of the shrimp, *Penaeus duorarum* Burkenroad. Intermediate host unknown. This is the "small gymnospored species of *Nematopsis*" which was found in shrimp with *N. duorarum* (the "large gymnospored species") but which was not produced by spores from the pelecypods. Florida, USA.

Nematopsis sp. Sprague, 1954 (179). In 1932, Pearse (142) reported the presence of "gregarine cysts" on the walls of the rectum of the calico crab *Eriphia gonagra* (Fabricius) collected at Dry Tortugas off the coast of Florida, USA. Sprague (179) expressed the opinion that this is a *Nematopsis,* not only because the limited description is characteristic of the porosporid gregarines but also because the best known species *N. legeri,* also occurs in a species of *Eriphia, E. spinifrons.*

Nematopsis sp. Vivarès & Rubió, 1969 (213). In gut of the crab *Ethusa mascarone.* Northeast coast of Spain (Blanes).

Nematopsis sp. Vivarès & Rubió, 1969 (213). In gut of the crab *Parthenope angulifrons.* Northeast coast of Spain (Blanes).

[*Nematopsis* sp. ?] "Gregarines" Cuckler & Fichter, 1939 (42). In the gut of the crab *Cancer productus.* Argyle Bay, San Juan Island, Washington, USA. Since this gregarine was found in a crab host and since as many as 3 nuclei were seen in 1 compartment (suggesting fusion of satellites), there is reason to suspect that it is a species of *Nematopsis.*

Genus *Pachyporospora* Théodoridès, 1961 (200).

Pachyporospora lamellaris (Bogolepova, 1953) Ormières, 1968 (141). Syns.: *Nematopsis lamellaris* Bogolepova, 1953 (18); *Tricystis plicata* Poljanskij & Chejsin, 1965 (52). In gut of a crab. Sea of Japan. Poljanskij and Chejsin (52), in their revision (1965) of Dogiel's (1951) book on protozoa, reproduced Bogolepova's (1953) sketch of this species and said it was from Dogiel (1951). They did not say where they got the name *Tricystis plicata* and we have been unable to find it elsewhere in the literature.

Pachyporospora laubieri Théodoridès, 1961 (200). In the gut of the crabs *Atelecyclus septemdentatus* Montagu (200) and *A. rotundatus* (213). Banyuls, France (200); northeast coast of Spain (213). TYPE SPECIES.

Pachyporospora retorta Ormières, 1968 (141). In gut of the crabs *Macropipus holsatus* (F.) (141, 214) and *M. vernalis* (213). Sète, France (141); coast of Tunisia (214); northeast coast of Spain (213).

Family and genus uncertain

Gregarina portuni Frenzel, 1885 (61). In gut of the crab *Macropipus* (= *Portunus*) *arcuatus.* Naples, Italy. Monocystid gregarine, certainly not genus *Gregarina* and unlike other known gregarines in decapods.

Gregarines, identity not specified. Heckmann (74) found intestinal gregarines in a number of decapods in Hawaii. Heldt (75) described, without naming, gregarines from the shrimp *Penaeus kerathurus* (Forskål) in the Gulf of Tunis. Théodoridès (202) judged that these last ones belonged to 2 species, a *Uradiophora* and a *Porospora.*

Poljanskij and Chejsin (52) mentioned "certain species of *Merogregarina* from the alimentary tract of crabs" but we have been unable to find mention of them elsewhere.

Subclass COCCIDIA Leuckart, 1879 (78).
Order EUCOCCIDA Léger & Duboscq, 1910 (78).
Family SELENOCOCCIDIIDAE Poche, 1913 (153).
Genus *Selenococcidium* Léger & Duboscq, 1909 (120).

Selenococcidium intermedium Léger & Duboscq, 1909 (120). In gut of European lobster *Homarus.* France. This is the type of the genus and the only species in the family. The authors described it only briefly in 1909 and more fully in 1910 (121).

Family AGGREGATIDAE Labbé, 1899 (107).
Genus *Aggregata* Frenzel, 1885 (61), emend. Léger & Duboscq, 1906 (114).

Aggregata coelomica Léger, 1901, emend. Léger and Duboscq, 1906 (114). Syn.: *Aggregata coelomica* Léger, 1901 [partim] (110, 114). In gut wall of the crab *Pinnotheres pisum* Penn., which lives in *Mytilus edulis* L. The original "species" eventually became in part the gregarine, *Cephaloidophora fossor.* France (English Channel) (110). Found recently by Vivarès and Rubió (213), in the same host, on the northeast coast of Spain.

Aggregata eberthi (Labbé, 1895) Léger & Duboscq, 1906 (115). Syns.: *Aggregata portunidarum* Frenzel, 1885 [partim] (61); *Benedenia eberthi* Labbé, 1895 (105) [cited by Labbé, 1899 (107), altho we can find no mention of this name in the 1895 paper]. Schizogonic stages in the portunid crabs *Macropipus* (= *Portunus*) *arcuatus* (61), *M. depurator* (115, 213), *M. tuberculata* (213), *M. bolivari* (213), *M. corrogatus* (214) and probably, *M. vernalis* (214). Sporogony in the cuttlefish *Sepia officinalis.* Common and widespread. Naples, Italy (61); Sète, France (115); Tunisia (214); northeast coast of Spain (213). Since the synonymy is quite complicated, only the most significant synonyms are given here. [See Labbé, 1899 (107) and Léger and Duboscq, 1908 (117) for more details.] Why the junior synonym *eberthi* was conserved instead of the original name *portunidarum* we have been unable to determine, altho the former is now fixed by the provisions of Art. 23(b) of the International Code of Zoological Nomenclature (82). We believe that this species, as Calkins (22) said, is the type; altho Pellérdy (143) said *A. octopiana* (Schneider, 1875) is the type. Our reasoning is that the former, being the only original species in genus *Aggregata,* must be type by monotypy as provided by Art. 68(c) (82). It may be pertinent, however, to note that the name *A. portunidarum* was originally applied inadvertently to 2 species, 1 a gregarine which later became *Nematopsis portunidarum.* This species has been the object of important life cycle studies by Léger and Duboscq (114, 115, 117), Pixell-Goodrich (150) and Dobell (49), and electron microscope studies by Porchet-Henneré and Richard (156, 157, 158).

Aggregata inachi Smith, 1905 (174), emend. Léger & Duboscq, 1906 (114). Schizogony stages in the gut wall of the crabs *Inachus dorsettensis* (174, 214) and *I. communissimus* (213); indistinguishable forms in *I. scorpio* (174). Stages in molluscan host unknown. Naples, Italy (174); coast of Tunisia (214); northeast coast of Spain (213). Smith, like earlier workers, presumed that the cysts in the gut wall belonged to a gregarine with free stages in the lumen, altho he saw only cysts of this species. Léger and Duboscq (114, 117) pointed out the incorrectness of this view.

Aggregata leandri Pixell-Goodrich, 1950 (152). Schizogony stages in gut wall of the shrimp *Leander squilla* L. Molluscan host unknown. Naples, Italy. Found also in the shrimp *Solenocera membranacea* (Risso) and *Acanthephyra eximia* Smith by Théodoridès (204) at Banyuls, France.

Aggregata vagans Léger & Duboscq, 1903, emend. Léger & Duboscq, 1906 (114). Syn.: *Aggregata vagans* Léger & Duboscq, 1903 [partim] (112). In gut wall of the crab *Eupagurus prideauxi* Leach. Banyuls, France. The original species eventually became in part the gregarine *Cephaloidophora ocellata.*

Aggregata sp. Léger & Duboscq, 1908 (117). In coelom of the crab *Pachygrapsus marmoratus* F. France (117). Found recently in the same host by Vivarès and Rubió on the northeast coast of Spain (213).

Aggregata sp. Setna & Bhatia, 1934 (173). Schizogony stages in gut wall of the shrimp *Parapeneopsis sculptilis* (Heller). Molluscan host unknown. Bombay, India.

Aggregata sp. Vivarès & Rubió, 1969 (213). Unidentified species of *Aggregata* were found in the crabs *Corystes cassivelaunus, Atelecyclus rotundus, Xantho poressa, Goneplax rhomboides, Parathenope angulifrons,* and *Macropodia rostrata.* Northeast coast of Spain.

Aggregata sp. Vivarès, 1970 (214). Unidentified species of *Aggregata* were found in the crabs *Carcinus mediterraneus, Dromia personata, Portumnus latipes, Xaiva biguttata, Macropipus vernalis, Pilumnus spinifer* and *Pilumnus hirtellus.* Coast of Tunisia.

Subphylum MICROSPORA Sprague, 1969 (188).

Class MICROSPOREA Corliss & Levine, 1963 (38).

Order MICROSPORIDA Balbiani, 1882 (6).

Family NOSEMATIDAE Labbé, 1899 (107).

Genus *Nosema* Nägeli, 1857 (135), emend. Pérez, 1905 (146).

Nosema frenzelinae Léger & Duboscq, 1909 (118, 119). Hyperparasite of the gregarine *Cephaloidophora conformis* (Diesing) in the crab *Pachygrapsus marmoratus* (Fabricius). France.

Nosema michaelis Sprague, 1970 (191). Syns.: *Nosema sapidi* DeTurk, 1940 [partim] (47); *N.* sp. Sprague, 1965 (182). In muscles of the crab *Callinectes sapidus* Rathbun. Atlantic and Gulf states of North America. A significant factor in crab mortality. DeTurk mistook spores of this species for sporoblasts of *N. sapidi.* Sprague et al. (187) made an electron microscope study of *N. michaelis.*

Nosema nelsoni Sprague, 1950 (177). Syn.: [non] *Nosema pulvis*: Jones (86). In muscles of penaeid shrimp. Widely distributed. First reported in *Penaeus aztecus* Ives in Louisiana, USA. Later found by Woodburn et al. (217), Hutton (80) and Hutton et al. (79) also in *P. duorarum* Burkenroad in Florida, USA. Recently found by Sprague and Vernick (189), who studied its fine structure, in *P. setiferus* from Georgia, USA. H. F. P. Champion (pers. com.) found a similar or identical species in the muscles of *Metapenaeus monocercos* in the Republic of South Africa. Kruse (pers. com.) reported *Nosema* sp., which may be identical with *N. nelsoni,* in the shrimp *Solenocera vioscai* and *Xiphopeneus krøyeri,* in Louisiana, USA.

Nosema pulvis Pérez, 1905 (145). In muscles of the crab *Carcinus maenas.* France. First described very briefly, this parasite was described more fully in the same year (146).

Nosema sapidi DeTurk, 1950, emend. Sprague, 1970 (191). Syn.: *Nosema sapidi* DeTurk, 1940 [partim] (47). In muscles of the crab *Callinectes sapidus* Rathbun. Beaufort, North Carolina, USA. This is distinguished from the other 3 species of *Nosema* described in muscles of decapods by having relatively large spores which (when stained) have light areas at the 2 ends and a dark band in the middle. DeTurk included in his description also *N. michaelis* Sprague, 1970 (191), the spores of which he mistook for sporoblasts of *N. sapidi.*

Nosema spelotremae Guyénot & Ponce, 1925 (66). Hyperparasitic in encysted metacercariae of the digenetic trematode *Microphallus* (= *Spelotrema*) *carcini* (198), which is parasitic in the crab *Carcinus maenas.* Stanier et al. recently (193) did an electron microscope study of this species.

Nosema sp. In 1963, one of us (V.S.) found a species similar to *N. spelotremae* in encysted microphallid metacercariae in a crab *Callinectes sapidus* collected in Pry Cove on the eastern shore of Chesapeake Bay, Maryland, USA. M. W. Newman (pers. com.) found a *Nosema,* possibly the same species also, in North Carolina, South Carolina and Georgia, USA, in 1969.

Genus *Gurleya* Doflein, 1898 (51).

Gurleya miyairii (Kudo, 1924) Sprague, 1970 (191). Syns.: *Thelohania* sp. Miyairi, 1909 (102); *Cocconema miyairii* Kudo, 1924 (102). In the muscles of 2 species of *Atyephira.* Japan.

Genus *Thelohania* Henneguy, 1892 (77).

Thelohania cambari Sprague, 1950 (178). In muscles of the crayfish *Cambarus bartoni.* Georgia, USA.

Thelohania contejeani Henneguy, 1892 (77). In muscles of the crayfish *Astacus fluviatilis* (77); *A. palipes* (53, 168) and *A. astacus* (53, 199). France (77); Germany (168); Russia (170) and Finland (199).

Thelohania duorara Iverson & Manning, 1959 (83). Syns.: *Thelohania hunterae* Jones, 1958 [nomen nudum] (86); *Thelohania* sp. Kruse, 1959 (99). In muscles of the shrimp *Penaeus duorarum* (83, 80, 84), *P. brasiliensis* (84) and *P. aztecus* (80). Florida, USA.

Thelohania giardi Henneguy, 1892 (77). In muscles of the shrimp *Crangon vulgaris.* France. TYPE SPECIES by subsequent designation, Gurley, 1893 (65).

Thelohania macrocystis Gurley, 1893 (65). In muscles of the shrimp *Palaemonetes varians.* Italy. Kudo (102) questioned the validity of this species.

Thelohania maenadis Pérez, 1904 (144). In muscles (usually) of the crab *Carcinus maenas.* Pérez (147) reported 1 case in which an ovary was parasitized, resulting in parasitic castration. This parasite, first reported briefly, was described more fully in 1905 (146). France (Arcachon).

Thelohania octospora Henneguy, 1892 (77). In muscles of the shrimp *Palaemon rectirostris, P. serratus* and *P. elegans.* France, England and the Black Sea (76, 77, 151).

Thelohania paguri Pérez, 1927 (148). In body cavity of the hermit crab *Eupagurus bernhardus.* France.

Thelohania penaei Sprague, 1950 (177). In gonad of the shrimp *Penaeus setiferus.* Louisiana, USA. H. F. B. Champion (pers. com.) found a similar or identical parasite in the ovary of *Penaeus indicus* in the Republic of South Africa.

Thelohania petrolisthis Sprague, 1970 (191). Syn.: *Thelohania* sp. Sprague, 1950 (177). In muscles of the crab *Petrolisthes armatus.* Louisiana, USA.

Thelohania sp. Sogandares-Bernal, 1962 (175). In muscles of the crayfish *Cambarellus schufeldi.* Louisiana, USA.

Thelohania sp. Thomas. (M. M. Thomas. Pers. com.) In gonad and muscles of the shrimp, *Penaeus semisulcatus* de Haan. South India.

Genus *Pleistophora* Gurley, 1893 (65).

Pleistophora cargoi (Sprague, 1966) Sprague, 1970 (191). Syn.: *Plistophora cargoi* Sprague, 1966 (183). In muscles of the crab *Callinectes sapidus* Rathbun. Maryland, USA.

Pleistophora miyairii (Kudo, 1924) Sprague, 1970 (191). Syns.: *Nosema anomalum* (?) Miyairi, 1909 (102); *Plistophora miyairii* Kudo, 1924 (102). In digestive tract of *Atyephira* sp. Japan.

Pleistophora sogandaresi (Sprague, 1966) n. comb. Syns.: *Plistophora* sp. Sogandares-Bernal (175); *Plistophora sogandaresi*

Sprague, 1966 (183). In muscles of the crayfish *Cambarellus puer* Hobbs. Louisiana, USA. Since *Plistophora* Labbé, 1899, is a junior synonym of *Pleistophora* Gurley, 1893 (186, 192), this species is transferred to the latter genus.

Pleistophora sp. Baxter, Rigdon & Hanna, 1970 (15). In the muscles of the shrimp *Penaeus setiferus* and *P. aztecus*. Galveston Bay, Texas, USA. Probably identical with *Plistophora* sp. Kruse, 1970 (191) found in the same host.

Pleistophora sp. Sprague, 1970 (191). In muscles of the shrimp *Palaemonetes pugio* Holthius. Georgia, USA.

Class HAPLOSPOREA Caullery, 1953 (27).
Order HAPLOSPORIDA Caullery & Mesnil, 1899 (24).
Family HAPLOSPORIDIIDAE Caullery & Mesnil, 1905 (25).
Genus *Minchinia* Labbé, 1896 (106).

Minchinia louisiana Sprague, 1963 (181). Syn.: *Haplosporidium* sp. Sprague, 1954 (179). In the gut wall of the mud crab, *Panopeus herbstii*. Louisiana, USA.

Minchinia sp. Rosenfield, Buchanan, Chapman, 1969 (162). In gill, muscles and gut tissue of the crab *Eurypanopeus depressus*. Virginia, USA.

Genus *Urosporidium* Caullery & Mesnil, 1905 (26).

Urosporidium crescens DeTurk, 1940 (48). Hyperparasitic in encysted metacercariae of a distome identified by DeTurk as *Spelotrema nicolli*, now in genus *Microphallus* (198). North Carolina (48); Maryland and Virginia (191), USA. Sprague (191) recently made observations on the structure of this species, Couch (41) studied its effect on its trematode host and Perkins (149) studied its ultrastructure.

Urosporidium sp. Sprague, 1970 (191). Hyperparasite in encysted metacercariae of *Microphallus* sp. in the shrimp, *Palaemonetes pugio*. Georgia, USA.

Subphylum CILIOPHORA Doflein, 1901 (78).

Class CILIATEA Perty, 1852 (78).
Subclass HOLOTRICHIA Stein, 1859 (78).
Order ASTOMATIDA Schewiakoff, 1896 (78).
Family ANOPLOPHRYIDAE Cépède, 1910 (28).
Genus *Anoplophrya* Stein, 1860 (136).

Anoplophrya minima Léger & Duboscq, 1909 (120). This very rare species of astome ciliate was reported from the posterior intestine and rectum of the lobster, *Homarus gammarus*. France.

Order HYMENOSTOMATIDA Dèlage & Hérouard, 1896 (78).
Suborder TETRAHYMENINA Fauré-Fremiet, 1936 (78).
Family COHNILEMBIDAE Kahl, 1933 (78).
Genus *Anophrys* Cohn, 1866 (34).

Anophrys maggii Cattaneo, 1888 (23). Syn.: *Anophrys sarcophaga* Cohn, 1866 (34). Occurring naturally, but rarely, in hemolymph of *Carcinus maenas*. Western coast of France (155). Poisson (155) stated that the parasitic *A. Maggii* of Cattaneo is identical with the free-living *A. sarcophaga* of Cohn, and thus the name *A. maggii* should be a junior synonym of *A. sarcophaga*. However, Tucker (14) argued that until more is known about these forms both names should be retained. Bang (14) was able to induce fatal experimental infections of *A. maggii* in *Carcinus maenas, Maia squinado* and *Macropipus depurator*. The ciliates within the hemolymph of these crabs were found to be eating host leukocytes. Bang (14) reported that the events leading to death in these *Anophrys*-infected crabs were anemia and asphyxiation followed by severe bacteremias.

Order APOSTOMATIDA Chatton & Lwoff, 1928 (78).
Family FOETTINGERIIDAE Chatton, 1911 (29, 32).
Genus *Synophrya* Chatton & Lwoff, 1926 (29, 32).

Synophrya hypertrophica Chatton & Lwoff, 1926 (32). Found in gills of the following marine crabs along the west coast of France: *Macropipus* (= *Portunus*) *depurator* at Banyuls and Roscoff, *M. puber* at Roscoff and Wimereux, *M. holsatus* at Roscoff, *M. pusillus* at Roscoff and Banyuls, *M. tuberculatus* at Banyuls, and *Carcinus maenas* at Roscoff. Recently found by Vivarès and Rubió (213) in *Macropipus tuberculatus, M. bolivari, M. depurator* and *M. vernalis* on the northeast coast of Spain. Vivarès (214) found the following decapods infected with *S. hypertrophica* in the Gulf of Tunis: *Dorippe lanata, Carcinus mediterraneus, Portumnus latipes, Macropipus arcuatus, M. corrugatus, M. vernalis, Pilumnus spinifer* and *P. hirtellus*. This apostome causes considerable pathogenesis in gills of hosts (32). Life cycle fully described and figured by Chatton and Lwoff (32).

Genus *Gymnodinioides* Minkiewicz, 1912 (130).

Gymnodinioides calkinsi Chatton & Lwoff, 1935 (32). Phoronts on the gills and trophonts on the cuticle of *Palaemonetes* sp. Woods Hole, Massachusetts, USA.

Gymnodinioides caridinae (Miyashita, 1933) Chatton & Lwoff, 1935 (32). Syn.: *Hyalospira caridinae* Miyashita, 1933 (132). Found on the "hairs" at base of antennules and on the gill filaments of *Xiphocaridina compressa* (freshwater shrimp of Japan), *Leander paucidens* and *Macrobranchium nipponense* by Miyashita in Japan. Reported as *Hyalospira caridinae* from *Palaemon varians* by Debaisieux (44) in Europe. Debaisieux gave a fairly detailed account of the life cycle of this species on the brackish water *Palaemon varians*.

Gymnodinioides inkystans Minkiewicz, 1913 (130). Phoronts on the gills and trophonts on the cuticles of *Eupagurus bernhardus, E. prideauxii* (130) and *Carcinus maenas* (32). Roscoff, France (32, 130). Also possibly observed by Minkiewicz, according to Chatton and Lwoff (32), on the following decapod genera: *Maia, Xantho, Porcellana* and *Galathea*. Trager (207) reported this species from the gills of *Pagurus longicarpus* at Woods Hole, Massachusetts, USA. According to Trager, the excystment of the phoronts of this species is synchronized with the molt of the host, and the conditions necessary to bring about excystment can be simulated in the laboratory.

Gymnodinioides sp. Chatton & Lwoff, 1935 (32). In the gastrovascular cavity of the anemone *Sagartia parasitica* found attached to *Eupagurus prideauxii*.

Gymnodinioides sp. Trager, 1957 (207). Phoronts on gills of *Uca pugnax*. Woods Hole, Massachusetts, USA. About 80% of the crabs examined were infested. Trager reported differences in this species and *G. inkystans* to be 10 or 11 ciliary bands rather than 9 as found on the latter. Also, this undescribed species had a more pointed and twisted posterior end than *G. inkystans*.

Genus *Phtorophrya* Chatton, Lwoff & Lwoff, 1930 (30).

Phtorophrya fallax Chatton, Lwoff & Lwoff, 1930 (30). A hyperparasite on the phoronts of *Gymnodinioides inkystans* on *Carcinus maenas*. Roscoff, France.

Phtorophrya insidiosa Chatton, Lwoff & Lwoff, 1930 (30). Usually found as a hyperparasite on the phoronts of *Gymnodinioides corophii* on amphipods, but in at least 1 instance (32) reported as a hyperparasite of *Gymnodinioides* sp. from *Carcinus*. Members of this genus are characteristically hyperparasitic or phoretic on the phoronts of other apostomes (32).

Genus *Polyspira* Minkiewicz, 1912 (130).

Polyspira delagei Minkiewicz, 1912 (130). On the gills of the following hosts: *Eupagurus bernhardus, Galathea squamifera,* and *Macropodia rostrata*. Roscoff, France. Found only in decapod crustaceans (32). Chatton and Lwoff were unable to transmit it easily to *Macropipus* sp. in the laboratory (32). These authors reported that this species is often found in company with *Gymnodinioides inkystans*.

Genus *Phoretophrya* Chatton, Lwoff & Lwoff, 1930 (31).

Phoretophrya nebaliae Chatton, Lwoff & Lwoff, 1930 (31). Altho usually found on the non-decapod *Nebalia geffroyi*, this species has also been reported from *Carcinus maenas* and *Macropipus holsatus*. Roscoff, France.

Genus *Terebrospira* Debaisieux, 1960 (44).

Terebrospira lenticularis (Debaisieux, 1957) Debaisieux, 1960 (44). Syn.: *Chattonia lenticularis* Debaisieux, 1957 (43). On the cuticle of *Palaemon varians* collected from the mouth of Schelde River (brackish water) in Western Europe (Netherlands). Debaisieux (44) gave the life cycle and host-ciliate relationship of this species in some detail. This species penetrates the cuticle of its host shrimp and thus can cause some damage.

Genus *Hyalophysa* Bradbury, 1966 (21).

Hyalophysa chattoni Bradbury, 1966 (21). Phoronts found on the gills and trophonts on the molts of several different species of decapods from the coasts of Washington and California, USA: *Pagurus hirsutiusculus*, *P. samuelis*, *P. granosimanus*, *P. alaskensis*, *Cancer oregonensis*, and *Lophopanopeus belli*. According to Bradbury, the genus *Hyalophysa* belongs to that group of apostomes phoretic on Branchyura, Anomura, Isopoda and Cirripedia which develop in the exuvial fluid of their hosts. Other ecologically related genera are *Gymnodinioides*, *Polyspira* and *Phoretophrya*. *H. chattoni* requires only 1 host for its entire life cycle.

Order CHONOTRICHIDA Wallengren, 1895 (78).

Family CHILODOCHONIDAE Poche, 1913 (153) emend. Mohr, 1948 (133).

Genus *Chilodochona* Wallengren, 1895 (215).

Chilodochona microchilus Wallengren, 1895 (215). On mouth parts of *Macropipus depurator*. Southern Sweden.

Chilodochona quennerstedti Wallengren, 1895 (215). On *Ebalia turnefacta* and *Macropipus depurator*. Southern Sweden (87). Mohr (133) divided the Order Chonotrichida into 3 families and pointed out that most chonotrichs found on decapod crustaceans are in the family Chilodochonidae.

Genus *Kentrochona* Rompel, 1894 (161).

Kentrochona nebaliae Rompel, 1894 (161). On the decapods *Ebalia turnefacta* and *Portunus depurator*. Southern Sweden. Also reported by Doflein (50) from Trieste and Rovigno, in the northern Adriatic.

Subclass PERITRICHIA Calkins, 1933 (78).

Order PERITRICHIDA Stein, 1859 (78).

Suborder SESSILINA Kahl, 1933 (78).

Family VORTICELLIDAE Ehrenberg, 1838 (140).

Genus *Vorticella* L., 1767 (136), emend. Ehrenberg, 1838 (140).

Vorticella verrucosa Dons, 1915 (55). Found on *Laomedia* sp. from Norway. Of many described species of *Vorticella* (87, 137, 140), this form is the only named vorticellid habitually found on decapods. Many species have been reported from non-decapod crustaceans.

Genus *Zoothamnium* Bory, 1826 (19).

Zoothamnium carcini Kent, 1881 (98). On *Carcinus maenas* from the south coast of England.

Zoothamnium procerius Kahl, 1933 (87). On legs of the crayfish *Astacus fluviatilis* from vicinity of Erlangen, Germany. Nenninger (137). reported a variety of this species, which she named *Z. procerius* var. *varius* from both gammarids and crayfish, but until subspecies names are more generally accepted for ciliates, this form is recognized as *Z. procerius*.

Zoothamnium sp. Ryder, 1883 (163). On "back and legs" of the oyster commensal decapod *Pinnotheres ostreum* Say. Maryland, USA. Ryder suggested that because the *Zoothamnium* supported on its "stalks" bacteria and "vibriones," it might be of benefit as a source of food to the oyster in which its crab host lives.

Family EPISTYLIDIDAE Kahl, 1933 (87).

Genus *Epistylis* Ehrenberg, 1832 (58).

Epistylis astaci Nenninger, 1948 (137). On the gills of *Astacus fluviatilis*. Germany.

Epistylis bimarginata Nenninger, 1948 (137). On legs of *Astacus fluviatilis*. Germany. Nenninger described this peritrich from the crayfish as a variety, *E. bimarginata* var. *urnula*, but again, until subspecific names are more generally accepted for ciliates this form is recognized only as a member of the species *E. bimarginata*.

Epistylis cambari Kellicott, 1885 (94). On gills of a species of *Cambarus*. Northeastern United States.

Epistylis niagarae Kellicott, 1883 (92). On body surface of crayfish (?) in freshwater. Northern United States.

Epistylis sp. Hutton, 1964 (80). On the commercial shrimp *Penaeus duorarum*. Numerous localities in Florida, USA.

Epistylis sp. Hutton, 1964 (80). On the deep-water shrimp *Hymenopenaeus robustus*, from 170 fathoms off Daytona Beach, Florida.

Epistylis sp. Pearse, 1932 (142). On gills of *Coenobita clypeastus*, at Garden and Long Keys, Florida, USA. On *Geograpsus lividus* and *Pachygrapsus transversus* in the Florida keys, USA.

Genus *Carchesium* Ehrenberg, 1832 (58).

Carchesium granulatum Kellicott, 1887 (95). On surface of freshwater crayfish of genus *Cambarus*. USA.

Family VAGINICOLIDAE de Fromentel, 1874 (62).

Genus *Vaginicola* Lamarck, 1816 (108).

Vaginicola paguri (André, 1910) Kahl, 1933 (87). Syn.: *Cothurnia paguri* André, 1910 (2). From cuticle of *Eupagurus bernhardus*. Roscoff, France.

Genus *Cothurnia*, Ehrenberg, 1832 (58).

Cothurnia astaci Stein, 1854 (195). On the branchial appendages of *Astacus fluviatilis*. Europe. Thought to be associated with mass mortalities of freshwater crayfish in Italy as reported by Ninni (139) and by Kent (98). Kent (p. 721) said, "During a fatal epidemic among the freshwater cray-fish of Lombardy and Venetia in the year 1863, it is reported by Ninni that the dying crustacea were completely infested with an Infusorium, referable to the genus Vaginicola, probably identical with the present species [*C. astaci*], its abnormal development on the branchial appendages apparently producing the death of the crustacean through asphyxia."

Cothurnia curva Stein, 1854 (195). From freshwater crayfish. Europe.

Cothurnia sieboldi Stein, 1854 (195). On the branchial appendages of the freshwater crayfish *Astacus fluviatilis*. Europe.

Cothurnia variabilis Kellicott, 1884 (93). Occurs by thousands on gills of crayfish *Cambarus affinis* (93) and *Astacus fluviatilis* (137).

Family LAGENOPHRYIDAE Kahl, 1935 (89).

Genus *Lagenophrys* Stein, 1852 (194).

This large genus of loricate peritrichs (52 species at present) is remarkable in that it has 22 species that are found only on decapod crustaceans and have strong host specificity.

Lagenophrys aegleae Mouchet-Bennati, 1932 (134). On the gills of the freshwater crayfish *Aeglea laevis*. Uruguay.

Lagenophrys articularis Nie & Ho, 1943 (138). On the antennae, legs, and swimmerets of *Palaemon nipponensis*. China.

Lagenophrys awerinzewi Abonyi, 1928 (1). On gills of the freshwater river crab *Telphusa fluviatilis*. Africa. Abonyi gave this lagenophryiid its specific name based upon the description of Awerinzew (5).

Lagenophrys bispinosa Kane, 1965 (91). On swimmerets of *Cherax rotundus setosus*. Stream near Newcastle, New South Wales, Australia.

Lagenophrys branchiarum Nie & Ho, 1943 (138). On the gills (only) of *Palaemon nipponensis*. China.

Lagenophrys callinectes Couch, 1967 (40). On both surfaces of the gill lamellae of the commercial, marine and brackish water crab *Callinectes sapidus*. From Chesapeake Bay, Maryland and Virginia; south to Gulf of Mexico estuarine waters wherever blue crab is found. During summer months infestations are so heavy that the gill surfaces of the crab may be completely covered.

Lagenophrys communis Kane, 1965 (91). On the telsons, swimmerets, and cuticles of the crayfish *Cherax destructor, C. albidus, Euastacus serratus, E. nobilis,* and *Engaeus* sp. Australia.

Lagenophrys darwini Kane, 1965 (91). On the gill filaments of *Cherax quadricarinatus*. Freshwater, near Darwin, northern Australia.

Lagenophrys deserti Kane, 1965 (91). In the branchial chambers and on gill filaments of *Cherax tenuimanus* and *C. quinquecarinatus*. Rivers in southeastern Australia.

Lagenophrys dungogi Kane, 1965 (91). On the gill filaments of a single specimen of *Euastacus* sp. Stream in Dungog, Australia.

Lagenophrys engaei Kane, 1965 (91). On brachiostegite membranes and gill filaments of crayfish *Engaeus victoriensis*, and on gill filament and gill bases of crayfish *Austroactacus hemicirratulis*. Near Melbourne, Australia.

Lagenophrys eupagurus Kellicott, 1894 (96). On gills of hermit crab *Eupagurus* sp. Woods Hole, Massachusetts, USA.

Lagenophrys latispinosa Kane, 1965 (91). On the flat surfaces of gills, gill bases and branchiostegite membranes. On *Cherax destructor* near Melbourne, Australia. On *C. destructor* and *C. albidus* from Victoria, Australia. On *C. rotundus* from New South Wales, Australia. Kane remarked that the loricae of many generations of this species are superimposed on one another on the cuticle of older hosts.

Lagenophrys lawrii Kane, 1965 (91). On flat surfaces of the gills of *Cherax quadricarinatus*. Near Darwin, Australia.

Lagenophrys lingulata Kane, 1965 (91). Found mostly on gill filaments, occasionally on the branchiostegite membranes. On *Cherax destructor* and *C. albidus* from Victoria, Australia, and on *C. rotundus* in central New South Wales, Australia. Type host and locality are *Cherax destructor* from around Melbourne, Australia.

Lagenophrys lunatus Imamura, 1940 (81). On body cuticle of shrimp *Leander paucidens* (83) and *Palaemon varians* (44). Japan (81); Belgium (44). One of us (J. C.) has found this species on *Palaemonetes vulgaris* from Chincoteague Bay, Maryland. Debaisieux (44) has done an excellent job of working out the life-cycle of this species.

Lagenophrys metopauliadis Corliss & Brough, 1965 (39). On the gill lamellae of a freshwater crab *Metopaulias depressus*. Jamaica. This was the 1st species of *Lagenophrys* to be reported from a brachyuran crab.

Lagenophrys occlusa Kane, 1965 (91). Restricted to the anterior portion of the branchial chambers of *Cherax destructor, C. albidus,* and *C. rotundus*. Victoria and New South Wales, Australia.

Lagenophrys rugosa Kane, 1965 (91). On the gill filaments of freshwater crayfish *Geocharax falcata*. Western Victoria, Australia.

Lagenophrys seticola Kane, 1965 (91). Original description based on specimens found on a land crayfish *Engaeus fultoni* from a burrow in a river bank near Melbourne, Australia. Found attached to setae, tail fan, swimmerets, gill base and edge of branchiostegites. Specimens referable to this species have also been found on *Cherax rotundus setosus, C. albidus, C. destructor* and *Euastacus nobilis* from Australia.

Lagenophrys spinosa Kane, 1965 (91). On the cuticle, swimmerets, telson and carapace of the crayfish *Cherax destructor*. Victoria, Australia.

Lagenophrys willisi Kane, 1965 (91). On gill filaments of freshwater crayfish *Cherax destructor, C. albidus* and *C. rotundus*. Australia.

Subclass SPIROTRICHIA Bütschli, 1889 (78).
Order HETEROTRICHIDA Stein, 1859 (78).
Suborder HETEROTRICHINIA Stein, 1859 (78).
Family FOLLICULINIDAE Dons, 1914 (54).

Members of this family belong to several different genera, all species of which are loricate. Species reported here as epibionts of decapods also may be, and usually are, found on substrates other than decapods and generally lack host specificity. Fauré-Fremiet (60) and Hadži (68) reviewed the species in this family and their various substrates.

Genus *Pebrilla* Giard, 1888 (63).

Pebrilla paguri Giard, 1888 (63). Found on the cuticle of *Pagurus bernhardus* by Giard, in 1888, at Pouliguen and at Roscoff, France. Later (1936), reported from cuticle of *Clibanarius misanthropus* from France by Fauré-Fremiet (60), who believed that, tho this species has features characteristic of members of genus *Folliculinopsis* Fauré-Fremiet,1936, its generic name *Pebrilla* should be retained.

Genus *Platyfolliculina* Hadži, 1938 (67).

Platyfolliculina paguri Andrews & Reinhard, 1943 (3). On the abdomen of hermit crab *Pagurus pubescens*. State of Washington, USA.

Genus *Metafolliculina* Dons, 1925 (56).

Metafolliculina andrewsi Hadži, 1938 (67). On *Pagurus floridanus* as reported by Andrews (4). Texas Gulf Coast, USA. Andrews stated that the tests of *M. andrewsi* were found on the abdominal filaments, and "large holding appendages." This species was also found on oyster shells in same region by Andrews.

Genus *Folliculinopsis* Fauré-Fremiet, 1936 (60).

Folliculinopsis gunneri (Dons, 1928) Fauré-Fremiet, 1936 (60). Syn.: *Folliculina gunneri* Dons, 1928 (57). Found by Fauré-Fremiet on the cuticle of sacculinid parasite of *Carcinus maenas* and *Porcellana platycheles*. France.

Genus *Folliculina* Lamarck, 1816 (108).

Folliculina viridis (Wright, 1858) Fauré-Fremiet, 1936 (60). Syn.: *Lagotia viridis* Wright, 1858 (218). Found on tegument of sacculinid parasite of *Carcinus maenas* and *Porcellana platycheles* along with *Folliculinopsis gunneri* (60). France.

Subclass SUCTORIA Haeckel, 1866 (69).
Order SUCTORIDA Claparède & Lachmann, 1858 (78).
Family PODOPHRYIDAE Haeckel, 1866 (69).
Genus *Podophrya* Ehrenberg, 1835 (59).

Podophrya astaci Claparède & Lachmann, 1861 (33). From the freshwater crayfish *Astacus fluviatilis*. Europe.

Genus *Paracineta* Collin, 1912 (37).

Paracineta homari (Sand, 1899) Kahl, 1934 (88). Syn.: *Acineta homari* Sand, 1899 (164). Found on an unidentified species of lobster, *Homarus*, and also on other decapods including *Pagurus* sp. Roscoff, France.

Family ACINETIDAE Stein, 1859 (196).

Genus *Acineta* Ehrenberg, 1833 (59), emend. Collin, 1912 (37).

Acineta constricta Collin, 1909 (36). On the legs of *Eupagurus cuanensis*. Cette (Sète), France.

Acineta sp. Couch, this paper. On the flat surfaces of gill lamellae of blue crabs, *Callinectes sapidus*. Chesapeake Bay, Maryland, USA, and Chincoteague Bay, Virginia, USA. This undescribed species is not common and occurs as solitary individuals attached near periphery of gill lamellae.

Family OPHRYODENDRIDAE Stein, 1867 (197).

Genus *Dendrosomides* Collin, 1906 (35).

Dendrosomides paguri Collin, 1906 (35). On the "long hairs" (setae) of the thoracic appendages of *Eupagurus excavatus* and *E. cuanensis*. Cette (Sète). France.

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7149

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Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies

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Abstract

Growth rates of anchovy larvae, *Engraulis mordax*, reared for 19 days under constant environmental conditions on a diet of laboratory-cultured organisms, exceeded the growth rates of anchovies fed on a diet of wild plankton. The rotifer *Brachionus plicatilis* was found to be a nutritous food source when fed to the larvae in concentrations of 10 to 20/ml and in combination with the dinoflagellate *Gymnodinium splendens* (100/ml). Optimum conditions were determined for mass culture of the rotifer. A high food concentration was the most important parameter needed to assure a high yield of rotifers. Large volumes (464 l) of the unicellular flagellate *Dunaliella* sp. were cultured for feeding the rotifers. The rotifer culture technique described produces approximately 2.5×10^6 organisms/day, providing a reliable food source for rearing studies. The lengths of *B. plicatilis* (without eggs) ranged between 99 and 281 μ, most rotifers being larger than 164 μ and less than 231 μ. Individuals weighed 0.16 μg and contained 8×10^{-4} cal.

Introduction

As part of a larger program on the biology of the northern anchovy *Engraulis mordax*, a study was initiated at the Fishery-Oceanography Center, La Jolla, California, USA, to rear larval anchovies using a variety of cultured food organisms. In an earlier report (Lasker et al., 1970) we showed that first-feeding anchovy larvae grew well initially on the cultured dinoflagellate *Gymnodinium splendens* (53μ diameter) but soon required a larger food organism. Veligers of the bubble snail *Bulla gouldiana* were of the proper size (140μ) and could be cultured in the laboratory, but growth rates of larval anchovies fed on them never reached those of larvae fed on a diet of wild plankton.

Because Japanese workers have used the mixohaline rotifer *Brachionus plicatilis* in fish culture, particularly for feeding larvae of the yellowtail *Seriola dorsalis* (Harada, 1970), we investigated the possibility of using this rotifer as food for larval anchovies. Although Ito (1960) published a study on factors affecting *B. plicatilis* reproduction in small cultures, he did not study reproduction in mass cultures which are needed to produce large numbers of rotifers to feed fish larvae.

Vasil'eva and Okuneva (1961) reared the rotifer *Brachionus rubens* in outdoor concrete tanks, but the environmental conditions were not controlled. In contrast to *B. plicatilis*, fecund female *B. rubens* attach to a substrate, therefore, only a portion of the latter's population is available as a forage organism.

In any rotifer culturing procedure, where the maximum number of individuals is desired, parthenogenetic (amictic) reproduction must be optimized and conditions avoided which cause sexual (mictic) reproduction, which produces smaller males and resting eggs. A number of factors are known to alter the ratio of mictic to amictic females; these are species composition and crowding (Gilbert, 1963), temperature, and the quantity and quality of algal food (Edmondson, 1965; King, 1966) and salinity (Ito, 1960). Quantitative studies are not yet available on the mass culture of rotifers, nor of a rotifer's nutritional adequacy with respect to larval fish growth, therefore, in this study we define laboratory conditions which can be used for mass culturing *Brachionus plicatilis* with the maximum production of amictic females. We compare reproduction of *B. plicatilis* on different algal diets, and assess the rotifer as a food for the larval anchovy *Engraulis mordax*.

Algal cultures

The algae we tried as rotifer food were *Monochrysis lutheri*, *Dunaliella* sp., *Nannochloris* sp. and *Exuviella* sp., obtained from Dr. W. H. Thomas of the Scripps Institution of Oceanography. The algae were unialgal, but not bacteria-free, and were cultured in 75% seawater (100% seawater = 33‰ S) containing soil extract (Lasker et al., 1970).

When large quantities of algae were desired, we chose to culture *Dunaliella* which we found to be compatible with the nutritional requirements of *Brachionus plicatilis* (p. 184), and the easiest of the 4 species to culture because it did not require vitamins or soil extract in the medium. *Dunaliella* medium was essentially the same as described by Thomas (1964). We prepared the seawater by filtering ultraviolet (UV) light-treated aquarium seawater through two Cuno Aqua-pure filters (pore size $= 5\mu$), a large capacity Millipore cartridge pre-filter and filter (pore size $= 0.45\,\mu$), and finally the water was re-irradiated with UV. EDTA (ethylenediamine tetracetate, disodium salt) 0.001%, was added with the nutrients. The medium was not autoclaved.

Twenty-liter carboys filled with 16 l of medium were inoculated with *Dunaliella* sp. The medium was bubbled with 5% CO_2 in air, stirred with a magnetic stirrer, and continuously illuminated between 500 and 700 ft-c at 23° to 25 °C. Fig. 1 illustrates the growth curve for a *Dunaliella* culture as measured by cell count, chlorophyll and phaeophytin production (Holm-Hansen et al., 1965). The cells increased from 3.4×10^3 to 3.0×10^6/ml in 9 days. The increase in the rate of phaeophytin production with a concomitant decrease in the rate of chlorophyll production indicates that the culture has reached its peak. At peak growth, the culture is used as an inoculum (p. 185) or $\frac{1}{4}$ of the culture can be withdrawn for rotifer feeding and replaced by fresh medium each day. Under the latter conditions the culture maintains a high cell density for 10 more days. The time to peak growth can be decreased from 9 to 4 or 5 days if the *Dunaliella* inoculum is increased to give a concentration of approximately 3×10^4 cells/ml.

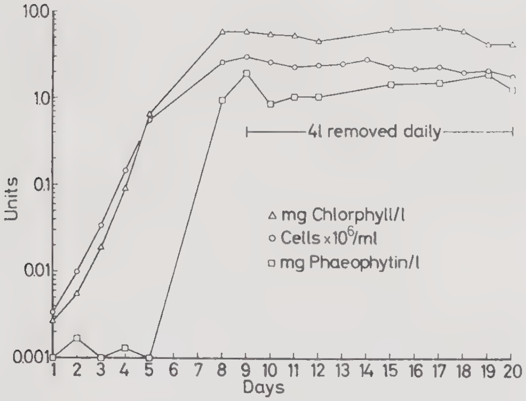

Fig. 1. Growth rate of *Dunaliella* sp. in a 16 l culture. The cell numbers increased from 3.4×10^3 to 3.0×10^6/ml in 9 days. At peak growth, $^1/_4$ of the culture is removed daily and replaced with fresh media. Using this procedure, a healthy culture with a sustained yield can be maintained for 10 more days

Culture conditions for *Brachionus plicatilis*

Temperature influences the fecundity of rotifers. Maximum reproduction of *Brachionus plicatilis* occurs between 30° to 34 °C. However, since the algae we used do not tolerate high temperatures, all experiments and culturing were performed between 21° and 25 °C.

Brachionus plicatilis doubling times at 24 °C were used to compare the effectiveness of 4 algae as food. King (1966) found that he required about 50 μg dry weight of algae/ml to maintain a maximum population size of the rotifer *Euchlanis dilatata*. In our experiments, therefore, we always fed *B. plicatilis* (similar in size to *E. dilatata*) an algal dry weight in excess of that used by King. Cell counts equivalent to 50 μg dry weight for the algae we used are: (1) *Dunaliella* sp. 0.3×10^6 cells/ml; (2) *Exuviella* sp. 0.2×10^6 cells/ml; (3) *Monochrysis lutheri* 1.5×10^6 cells/ml (Parsons et al., 1961). There is no weight data available for *Nannochloris*, therefore, because it is smaller than *Monochrysis*, higher cell concentrations were used. All algal cells were counted with a Coulter Counter, Model A.

In the initial experiments (Table 1), 10 or 100 female rotifers with eggs were inoculated into cultures of each of the algae listed above, when algal cell growth was in the logarithmic phase and the number of cells was 0.6 to 4×10^6/ml, depending on the species. Algae were added as necessary to maintain a constant cell density. *Brachionus plicatilis* individuals were counted at different time intervals from 4 to 17 days.

In a second series of experiments, 2,000 rotifers of all sizes were added to algal flasks and counted after 4 days.

Doubling times were calculated by dividing $\log_e 2$ by the instantaneous growth rate (K)

$$K = \frac{\log_e N_t - \log_e N_o}{t} \tag{1}$$

where N_o is the number of rotifers in the inoculum, N_t is the final number after time t in days.

Doubling times ranged from 0.8 to 1.1 days at 24 °C. There were no obvious differences in reproductive rates between rotifers feeding on different algal diets of similar dry weights (Table 1).

Dunaliella sp. was used as the main diet to determine the relationship between the doubling time and the concentration of algae. Only female rotifers with eggs were used for the original inoculum. Algal cell concentration was varied from 1.0×10^5 cells/ml to 1.0×10^6 cells/ml (Table 2). Doubling times decreased from almost 3 days to about 1 day, with a tenfold increase in algal cells.

The reproductive rate of *Brachionus plicatilis* was the same in 25 and 33‰ S seawater, provided food concentrations were comparable. Consequently, we used the latter salinity for mass culturing the rotifers. When cultures became dense with *B. plicatilis* we noted no decrease in doubling times as long as food was in excess, and we concluded that crowding, up to 200 rotifers/ml (Tables 1 and 2), did not inhibit reproduction in this species.

Table 1. *Brachionus plicatilis. Reproductive rates of rotifers fed on 4 algal diets, at 24 °C*

Diet	Cell concentration (No/ml)	Initial number of rotifers (N_o)	Final number of rotifers (N_t)	Time in days (t)	Instantaneous growth rate (K)	Doubling time (days)	Final concentration of rotifers (No/ml)	Container size (ml)
Monochrysis lutheri	3×10^6	10	36×10^3	12	0.68	1.0	18	2000
		10	130	4	0.64	1.1	1	100
		2000	42×10^3	4	0.76	0.9	200	2000
Nannochloris sp.	4×10^6	10	16×10^3	12	0.62	1.1	8	2000
		10	270	4	0.82	0.8	3	100
		2000	30×10^3	4	0.68	1.0	152	2000
Exuviella sp.	6×10^6	10	190	4	0.74	0.9	2	100
		35	12×10^4	17	0.61	1.1	60	2000
Dunaliella sp.	1×10^6	10	54×10^3	13	0.66	1.1	27	2000
		10	230	4	0.78	0.9	2	100
		2000	45×10^3	4	0.78	0.9	220	2000

Table 2. *Brachionus plicatilis. Reproductive rates of rotifers fed on several concentrations of Dunaliella sp. at 24 °C*

Diet	Cell concentration (No/ml)	Initial number of rotifers (N_o)	Final number of rotifers (N_t)	Time in days (t)	Instantaneous growth rate (K)	Doubling time (days)	Final concentration of rotifers (No/ml)	Container size (ml)
Dunaliella sp.	1×10^5	80	900	10	0.24	2.9	0.5	2000
	1×10^5	80	850	8	0.30	2.3	0.4	2000
	1×10^5	7	90	10	0.26	2.7	0.9	100
	2×10^5	20	3×10^4	20	0.37	1.9	15	2000
	2×10^5	20	6×10^4	20	0.40	1.8	30	2000
	1×10^6[a]	100	93×10^3	9	0.76	0.9	46	2000

[a] See Table 1 for additional data.

Mass culture of *Brachionus plicatilis*

To mass culture rotifers, a large volume of *Dunaliella* sp. was needed. The fiberglass water tables, available in the Fishery-Oceanography Center aquarium (LASKER and VLYMEN, 1969), were filled to a depth of 13 cm (464 l) with *Dunaliella* medium and inoculated with 32 l of a culture of *Dunaliella* which gave a final concentration of 2×10^5 cells/ml. Water-table cultures were aerated and kept under constant illumination (140 to 170 ft-c). Temperature was not controlled, but aquarium temperatures were relatively constant and only varied between 21° and 25 °C. When the number of *Dunaliella* cells reached 1×10^6/ml (usually in 2 to 4 days) rotifers were added. With such heavy concentrations of *Dunaliella* it was rare to find any other species of algae contaminating the culture during the first few weeks.

An inoculum of 2×10^4 rotifers yielded 2.5×10^6 rotifers/day after 4 or 5 days. The rotifers were harvested daily for about a month, but the production rate decreased, as the alga was consumed faster than it reproduced; therefore, 4 l of *Dunaliella*, from the 16 l cultures, were added as necessary.

Alternatively, rotifers could be kept at 13° to 17 °C in a 500 l holding tank for months provided they were fed *Nannochloris* at a minimum concentration of 1×10^6 cells/ml. Aeration, 200 ft-c illumination for 14 h/day, and addition of enough nutrients for 500 l of medium monthly were required. *Brachionus plicatilis* reproduces slowly at this temperature, maintaining a constant density, thus assuring a continuous source.

Rotifers were collected for feeding fish larvae by slowly circulating the water with a submersible pump through a plastic tube, one end of which was covered with 64 μ mesh netting (Nitex).

Size, weight and caloric content of *Brachionus plicatilis*

Our clone of *Brachionus plicatilis* was isolated from the Salton Sea by Dr. I. HAYDOCK of the Southern California Water Research Project. The size of the individuals (without eggs) resulting from this clone ranged between 99 to 281 μ long and 66 to 182 μ wide, with about 80% of the population between 164 to 231 μ long and 99 to 149 μ wide. Attached eggs add about 90 μ to a rotifer's length.

Dry weights averaged 0.16 ± 0.01 μg/individual in 4 determinations. Weights were determined by collecting a known number of rotifers on a washed and tared Nitex (nylon 35 μ mesh) circle which had been cut to fit a 25 mm Millipore filter holder. The rotifers were washed with distilled water, dried to a constant weight at 60 °C, and weighed with a Cahn electrobalance to ±2 μg. The samples were scraped off the Nitex, pelleted and subsequently used for calorie and ash measurements.

The caloric content was measured with a Parr 1411 non-adiabatic calorimeter. Benzoic acid was added to the samples weighing less than 40 mg. The average of 4 determinations, converted to ash-free values, was 5335 ± 139 cal/g dry weight organic substance.

The amount of ash was estimated by incinerating samples in a muffle furnace at 500° to 525 °C. The mean for 7 measurements was 7.8 ± 2.0% ash on a dry weight basis.

Rearing anchovy larvae on a rotifer diet

The rearing methods we used were the same as described by LASKER et al. (1970). Anchovy eggs were collected at sea and sorted into the experimental containers at 17 °C. Both small, 10 l containers, with 100 eggs in each and large, 510 l tanks containing 2,000 to 4,000 eggs were used for assessing the feeding conditions necessary for maximum growth. The large tanks were initially filled half full to reduce the quantity of food organisms required, and gradually filled to capacity when the rotifer production exceeded the daily demand.

The growth rates of the rotifer-fed larvae were compared with larvae fed veligers and wild plankton (LASKER et al., 1970; KRAMER and ZWEIFEL, 1970). The mean larval standard length after 19 days on each experiment diet was the criterion for determining the adequacy of the diet.

Growth of anchovy larvae in small containers

Data on the length achieved by *Engraulis mordax* in rearing experiments on each of 4 feeding regimes using rotifers as the basic food and the previous results where veliger and wild plankton diets were used (LASKER et al., 1970) are summarized in Table 3. *Gymnodinium splendens* (100/ml) was added as the first food (except in Group II) followed by the test organism on the 4th day after hatching (hatching = day 0). *Dunaliella* sp. at a density of 1×10^5 cells/ml was added to the larval fish rearing containers to maintain the rotifers in a well-fed condition. Anchovy larvae do not feed on *Dunaliella* sp.

In the first experiment (Group II) rotifers were used as the only food for *Engraulis mordax*. About 7% of the individuals in a *Brachionus plicatilis* culture are 80 μ or less in width, which is an acceptable size for first feeding anchovy larvae (BERNER, 1959). Thus, at a rotifer concentration of 15 to 20/ml, at least 1 rotifer/ml was of a satisfactory size for larval anchovy initial feeding. There was a high mortality of the larvae in the first 9 days which correlated with the mortality curves for starving larvae (LASKER et al., 1970), unlike experiments where *Gymnodinium splendens* was added. However, the final mean length, 7.8 mm, of the few larvae which succeeded in capturing enough prey during the first days of feeding was significantly larger ($p = < 0.05$) than the mean length, 7.0 mm, for veliger-fed larvae (Group I).

In the next series of tests, rotifers were fed to the larvae in progressively increasing concentrations and in combination with *Gymnodinium splendens*. We tried to maintain food densities which could be compared with the earlier wild plankton and veliger experiments (LASKER et al., 1970) and also included a high rotifer density experiment. With each increase in the concentration of rotifers offered as food for the larvae, there was a significant increase in the resulting size of the larval anchovies (see probabilities, groups III, IV, V, Table 3).

In Group III, the rotifer concentration varied between 2 to 6/ml, averaging about 3 to 4/ml. Survival at this food density was very low, similar to the *Brachionus plicatilis* only diet (Group II); however, the larvae were significantly larger than veliger-fed larvae ($p = < 0.01$), averaging 8.2 mm standard length.

In Group IV, the concentration of food offered to the larvae and the percent survival of the larvae were comparable to the veliger experiments (Group I). The rotifer densities varied between 2 to 10/ml and averaged about 7/ml. The combined larval mean length, 8.6 mm, was greater than the mean length achieved with a veliger food ($p = < 0.01$) and also greater than the length attained on the lower density rotifer diet (Table 3).

The best larval anchovy growth rates were attained in the high food density experiments, Group V, when 10 to 20 rotifers/ml were fed. Although there was a difference between two treatments within this group — Table 3 (Va) 8.9 mm differed from (Vc) 9.5 mm ($p = < 0.01$) — it is quite clear that a high food density should be maintained for larvae feeding on rotifers. The Group V mean larval length, 9.1 mm, is the greatest we have obtained in small containers on cultured food. It is significantly larger ($p = < 0.01$) than all other experimental diets except for a diet of wild plankton (Table 3). The average anchovy growth rate for 19 days in 10 l containers on the high density rotifer diet is 0.31 mm/day as compared to 0.38 mm/day for wild-plankton-fed larvae.

Table 3. *Growth and survival of anchovy larvae (Engraulis mordax) after 19 days on experimental diets, in small containers, at 17°C*

Group	Diet	Food density (No/ml)	Number of larvae	Mean larval length (mm)	Standard deviation (mm)	Range in individual lengths (mm)	Group mean length (mm)	Survival (%)	Probabilities for equal lengths between groups
I[a]	*Gymnodinium splendens*	100—200	121	7.0	1.1	4.9 – 9.6		12—47	
	Veligers	6—8							
II	*Brachionus plicatilis*	15—20	12	7.8	1.0	6.1— 9.8		14	II vs I – p = < 0.05
III	*Gymnodinium splendens*	100							III vs II –p = < 0.05
	Brachionus plicatilis	2—6 a)	18	8.5	0.7	6.7— 9.7		18	
		b)	9	8.3	0.8	7.3— 9.7	8.2	9	
		c)	48	8.1	1.1	6.0—10.3		—	
IV	*Gymnodinium splendens*	100							IV vs III – p = < 0.05
	Brachionus plicatilis	2—10 a)	18	8.0	1.4	5.9— 9.8		19	
		b)	44	8.7	1.5	5.8—11.7	8.6	52	
		c)	40	8.8	1.8	6.1—13.3		41	
V	*Gymnodinium splendens*	100							V vs IV – p = < 0.01
	Brachionus plicatilis	10—20 a)	37	8.9	1.1	6.6—11.0		39	
		b)	29	9.0	1.5	5.9—11.6	9.1	—	
		c)	40	9.5	1.0	6.9—11.8		43	
VI[a]	Wild plankton	2	12	10.5	1.4	8.1—13.0			VI vs V – p = < 0.01

[a] Data from LASKER et al. (1970).

Table 4. *Length of anchovy larvae (Engraulis mordax) after 15 and 19 days on experimental diets in large tanks*

Group	Diet	Food density (No/ml)	Age (days)	Number of larvae	Mean larval length (mm)	Standard deviation (mm)	Range in individual lengths (mm)	Container size (l)	Temperature (°C)
I	*Gymnodinium splendens*	50—100							
	Brachionus plicatilis	4—8	15	20	8.4	1.3	5.9—10.7	510	17.0
	Artemia, day 15	<1	19	10	10.1	0.8	8.9—11.1		17.0
II	*Gymnodinium splendens*	50—100							
	Brachionus plicatilis	10—20	15	20	10.5	0.8	9.0—11.8	510	17.0—18.0
	Artemia, day 15	<1	19	20	12.0	1.2	9.4—13.9		17.0—18.1
III	Wild plankton[a]	<1—>2	15	51	8.8	1.2	5.8—11.1	380	17.0
	Artemia, day 17	<1	19	35	10.6	2.1	5.5—13.7		17.0

[a] Data from KRAMER and ZWEIFEL (1970). The 15 and 19 day mean lengths of the larval anchovies reared on a wild-plankton diet were obtained by combining KRAMER and ZWEIFEL's data for days 14, 15 and 16, and for days 18 and 20.

Growth of anchovy larvae in large containers

Two thousand *Engraulis mordax* eggs were used in the first experiment, and the larvae were reared at 17 °C on a diet of *Gymnodinium splendens* and rotifers at 4 to 8/ml. *Dunaliella* sp. was added to supply the rotifers with food (1×10^5 cells/ml), and the diet was supplemented with newly hatched *Artemia* nauplii from the 15th day. The mean lengths achieved by larvae on the 15th and 19th day of this diet were compared with KRAMER and ZWEIFEL's (1970) results on anchovies reared at 17 °C on a diet of wild plankton (1 to 2 organisms/ml), and supplemented with *Artemia* nauplii from the 17th day. The growth rates on both diets were the same. The growth attained on days 15 and 19 for rotifer-fed larvae, 8.4 and 10.1 mm, did not differ significantly from the wild-plankton-fed larvae, 8.8 and 10.6 mm (Table 4).

In a second experiment, 4,000 laboratory-spawned and fertilized anchovy eggs (LEONG, 1971) were added to the large tank. The feeding regime was the same as in the first trial except that the rotifer concentration was doubled, to test the results obtained from the high density small container experiment. The temperature held at 17 °C for 10 days and, due to a failure in the temperature control, the tank warmed to 18 °C on the 15th day and was 18.1 °C on day 19. The mean length of the larvae on this high-density rotifer diet (10 to 20/ml) was significantly ($p = < 0.01$) greater than the wild plankton control (Kramer and Zweifel, 1970) on both the 15th and the 19th day (Table 4). The average growth rate of the rotifer-fed larvae for 19 days was 0.46 mm/day, or 0.07 mm/day more than the wild plankton-fed larvae. The success of this trial can be attributed to the increased food ration, although there may have been some effect from the higher temperature.

In conclusion, laboratory cultured rotifers, fed in high concentrations, appear to be a nutritious food source for anchovy larvae. For the first time in our experience, the larval anchovy early growth rate on a diet other than that of wild plankton equalled and exceeded that of larvae fed on wild plankton.

Summary

1. Optimum conditions for mass culturing the rotifer *Brachionus plicatilis* are described. The time for the rotifer population to double in size was determined at different temperatures, salinities, food concentrations, and on various algal diets. A high food concentration was the most important parameter needed to assure a high yield of rotifers. Under the conditions given, 2.5×10^6 rotifers can be harvested daily.

2. A technique is described for culturing large volumes of the marine flagellate *Dunaliella* sp. Dense, 16 l cultures with 3×10^6 cells/ml were used as the inoculum for a 464 l tank in which the rotifers were cultured. Cell concentrations in the large tanks increased to 1×10^6/ml in 2 to 4 days.

3. *B. plicatilis* is evaluated as a food for larval anchovies. The mean lengths of anchovies (*Engraulis mordax*) after feeding for 19 days on rotifer diets are compared with previous experiments in which either gastropod veligers or wild plankton were fed. Even at a very low density of 3 to 4/ml, rotifers are a more valuable food source for the larvae than veligers at a concentration of 6 to 8/ml. Larval growth rates obtained on the highest density diet (10 to 20 rotifers/ml) exceeded the wild plankton controls.

4. The size of *B. plicatilis* (without eggs) ranged between 99 to 281 µ long and 66 to 182 µ wide. The dry weight averaged 0.16 µg/individual, ash was 7.8% of the dry weight, and caloric content 5335 cal/g dry organic substance.

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7150

ESTIMATING PHYTOPLANKTON PRODUCTION FROM AMMONIUM AND CHLOROPHYLL CONCENTRATIONS IN NUTRIENT-POOR WATER OF THE EASTERN TROPICAL PACIFIC OCEAN[1,2]

William H. Thomas[3] and Robert W. Owen, Jr.[4]

ABSTRACT

Previous work has shown that nitrogen is the limiting nutrient in poor (nitrate-free) water in the eastern tropical Pacific Ocean and has suggested that ammonium is the principal nitrogen source for phytoplankton in this water. Enrichment and uptake experiments with various concentrations of ammonium have provided values for the half-saturation constant, K_S, and the maximum growth rate, μ_{max}, which can be used to calculate actual growth rates with the hyperbolic model relating growth rate to limiting nutrient concentration. At two stations, growth rates calculated from ammonium concentration agreed well with those calculated from chlorophyll and ^{14}C production, and the hyperbolic equation could be combined with that using production and chlorophyll to calculate production alone. In this paper calculated production rates are compared with those observed from ^{14}C uptake measurements for a number of EASTROPAC cruises. The regression between calculated production and observed production is highly significant and the slope is close to 1.0, indicating reasonable agreement, particularly when all of the errors in the calculation, especially in K_S, are considered. The results suggest rather close control of phytoplankton production by the limiting nutrient, ammonium, in these near-surface, nutrient-poor waters.

This paper describes how concentrations of a limiting nutrient in sea water and some measure of the standing crop of phytoplankton can be used to estimate phytoplankton production. Estimated production is compared with observed ^{14}C production, and the two sets of values are shown to agree reasonably well when all the errors in the estimation are considered.

The EASTROPAC Expedition series has delineated particularly well areas that are rich in nutrients and that are nutrient-poor in the eastern tropical Pacific Ocean. Rich areas include the Peru Current, the Costa Rica Dome, and an area of equatorial upwelling extending across the EASTROPAC area (from the American coast to long 119° W). Poor areas lie to the north and south of the equatorial upwelling zone and to the west of the Peru Current and Costa Rica Dome. Rich and poor near-surface waters were mapped in previous papers (Thomas, 1969, 1970b) and will be shown in detail in the EASTROPAC Atlas (Thomas, unpublished data). Nutrient values for rich and poor water are also given in Table 1 of Thomas (1970a).

Corresponding areal and seasonal changes in the phytoplankton production in this region have been observed and attributed in part to mechanisms of nutrient supply (Owen and Zeitzschel, 1970). No accounting has been possible, however, for the variations observed within the nutrient-poor surface layer of the region.

Near-surface water in poor areas is especially low in nitrate-nitrogen; this nutrient is generally not detectable (<0.1 μg-at./liter). Ammonium-N is present in concentrations ranging up to 1 μg-at./liter and organic nitrogen can reach

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concentrations of 17 μg-at./liter, but this latter nitrogen source is probably not utilized by phytoplankton (Thomas, Renger, and Dodson, in press).

Prior to EASTROPAC (pre-1967) low nitrate/phosphate ratios in tropical Pacific poor water suggested that nitrogen was a limiting nutrient although ratios were increased when ammonium was included along with nitrate, and it was suggested that this latter nutrient alleviated N deficiency (Thomas, 1966).

Recent EASTROPAC enrichment experiments provided direct evidence for N limitation. Phytoplankton growth occurred in experiments where nutrients were added singly to sea water samples only with N addition, and if N was deleted from an otherwise complete enrichment, little or no growth resulted (Thomas, 1969, 1970b). The fact that photosynthetic assimilation ratios were only slightly (but significantly) decreased in poor water as compared with rich water testified further to the alleviation and control of deficiency by ammonium (Thomas, 1970a).

Having established which nutrient is commonly limiting, one can use a quantitative nutrient requirement in an appropriate mathematical model to estimate growth rates (production) from concentration of the limiting nutrient. Recent work (Caperon, 1967; Dugdale, 1967) indicates that the best model is hyperbolic:

$$\mu = \mu_{\max} \left(\frac{S}{K_s + S} \right) \qquad (1)$$

where μ is the phytoplankton specific growth rate, $\mu_{\max}$ is the maximum rate which is unlimited by low nutrient concentration, S is a measured limiting nutrient concentration in sea water, and K_s is the "half-saturation constant"—a nutrient concentration that supports a rate equal to $\mu_{\max}/2$. This equation is equivalent to the Michaelis-Menton formulation for enzyme kinetics and was first applied to bacterial growth rates by Monod (1942). Many biological processes follow the hyperbolic model and since growth is the result of a series of coupled enzymatic reactions, the hyperbolic model is the model of choice.

A previous paper (Thomas, 1970b) provides information on $\mu_{\max}$ and K_s (for ammonium) from which μ can be calculated. To obtain these values we enriched samples of nutrient-poor Pacific sea water from a depth of 10 m with a complete mixture of non-nitrogenous nutrients to which various concentrations of ammonium were added. The samples were then incubated in natural light approximating the intensity that would be found at 10 m depth. Growth was estimated by successive daily measurements of *in vivo* chlorophyll (Lorenzen, 1966) in each treatment, and rates integrated over a daily period were calculated from the maximum increases in chlorophyll. These rates were plotted against ammonium concentrations to fit a hyperbolic model and values of K_s and $\mu_{\max}$ were obtained from the plot. These values and their 95% confidence limits are given in Table 1 for two such experiments. K_s values can also be determined from uptake experiments since recent work has shown that K_s values for growth and uptake are equivalent (Eppley and Thomas, 1969). Also included in Table 1 are uptake K_s values obtained by MacIsaac and Dugdale (1969) for nutrient-poor tropical Pacific water. Their values for $V_{\max}$, the maximum uptake rate, are not equivalent to $\mu_{\max}$ and thus are not included

TABLE 1.—Rate parameters for growth and uptake on ammonium in nutrient-poor tropical Pacific sea water.

Cruise	Station	K_s (μM)	95 percent limits	$\mu_{\max}$ (Doublings/day)	95 percent limits	Reference
EASTROPAC 76	007	1.68	± 3.28	1.12	± 0.83	Thomas (1970b)
EASTROPAC 76	173	1.47	± 0.91	1.22	± 0.27	Thomas (1970b)
Thompson 26	15	0.10	--	--	--	MacIsaac and Dugdale (1969)
Thompson 26	36	0.55	--	--	--	MacIsaac and Dugdale (1969)
Te Vega 13	651-a	0.62	--	--	--	MacIsaac and Dugdale (1969)
Mean values		0.88		1.17		
95 % limits of mean		1.33		0.14		

in Table 1. It will be noted that confidence limits for K_S values in given experiments are large as is the confidence limit for the mean of all five values which is used in subsequent calculations (see Results and Discussion). This can be attributed to lack of precision in measuring either growth or uptake; even in controlled experiments with laboratory cultures, K_S values are imprecise (Eppley, Rogers, and McCarthy, 1969; Eppley and Thomas, 1969).

The integrated daily growth rate, μ, can also be calculated from ^{14}C production estimates and chlorophyll concentrations using the following equation:

$$\mu = \frac{3.32\ [\log_{10}(R \cdot \text{chl} + \text{Prod}) - \log_{10}(R \cdot \text{chl})]}{1\ \text{day}} \qquad (2)$$

as has been done for laboratory cultures by Thomas (1964) and McAllister, Shah, and Strickland (1964). In this equation R is the carbon/chlorophyll ratio; $R \cdot \text{chl}$ thus is the standing stock of phytoplankton carbon. The constant 3.32 converts logarithms to the base 10 to logarithms to the base 2 and allows μ to be expressed as doublings of phytoplankton carbon per day.

In the previous paper (Thomas, 1970b), μ calculated from ammonium (equation 1) was compared with μ calculated from ^{14}C production and chlorophyll (equation 2) for the two EASTROPAC stations where K_S and $\mu_{\max}$ were determined from enrichment experiments. At station 76.007, μ calculated from ammonium was 0.385 doublings/day while that calculated from ^{14}C uptake and chlorophyll was 0.365 doublings/day. At station 76.173 both values were identical—0.276 doublings/day. For the calculation we used an R value of 98, that found by Eppley (1968) for nitrate-free water off La Jolla.

This excellent agreement suggested that we could set equation (1) equal to equation (2) and solve for production as a function of ammonium and chlorophyll using K_S and $\mu_{\max}$ as constants. The new equation thus derived is

$$\text{Prod} = \text{chl} \cdot R \left[\text{antilog}\left(\frac{\mu_{\max}}{3.32} \cdot \frac{S}{K_s + S} \right) - 1 \right] \qquad (3)$$

This expression allows a direct comparison calculated and measured ^{14}C production (see Results and Discussion).

METHODS

Methods for determining K_S and $\mu_{\max}$ were given previously (Thomas, 1970b; MacIsaac and Dugdale, 1969)—see also the previous section. Chlorophyll and production samples were taken from the depth of the 50 % light level, which was always in the upper mixed layer and varied from 9 to 16 m. This depth was determined by multiplying the depth at which the Secchi disc disappeared by 0.38. This factor employs the assumption that the Secchi disc disappears at 16 % of surface light intensity (Strickland, 1958).

Chlorophyll was determined in these samples by filtration on glass fiber filters, followed by 90 % acetone extraction of the filters, and measurement of fluorescence of the extract (Yentsch and Menzel, 1963; Holm-Hansen, Lorenzen, Holmes, and Strickland, 1965) using equations developed by Lorenzen (1966).

Simulated *in situ* production was measured by adding 20 μc $Na_2{}^{14}CO_3$ solution to the samples (Steemann Nielsen, 1952) and incubating them in a tubular shipboard incubator space in which natural light intensity was attenuated to 50 % of that incident. Incubation was started at noon and continued until sunset at sea surface temperature. Following incubation the samples were filtered through HA Millipore®[5] filters and their radioactivity assayed ashore by G-M counting of the filters. The ^{14}C solution was standardized by liquid scintillation counting and the efficiency of the G-M counter for these filters was determined by combusting some of these and measuring the evolved $^{14}CO_2$ with an ionization chamber. Daily uptake was determined by multiplying the activity by 2; we also corrected for the isotope effect by multiplying by 1.05. Darkened samples were incubated with illuminated samples and dark uptake was subtracted from light uptake. No corrections for respiration by phytoplankton were made.

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[5] The use of trade names is merely to facilitate descriptions: no endorsement is implied.

Ammonium was measured ashore in frozen samples from a depth of 10 m by the method of Richards and Kletsch (1964). Some labile amino-N which is probably available to phytoplankton is measured along with ammonium by this method.

RESULTS AND DISCUSSION

For the comparison of calculated and measured ^{14}C production, we have used samples from 10 m incubated at light intensities approximating those at 10 m to determine K_s and μ_{max}, and actual ^{14}C values from the 50% light level. We did this so that light intensities would not be a factor in the comparison—that is, light was presumed to be at saturating intensities but not inhibitory, which would be the case if surface samples had been incubated in the growth experiments and compared with surface production.

Ammonium was not determined at all production stations, and we selected those production values where data were available for

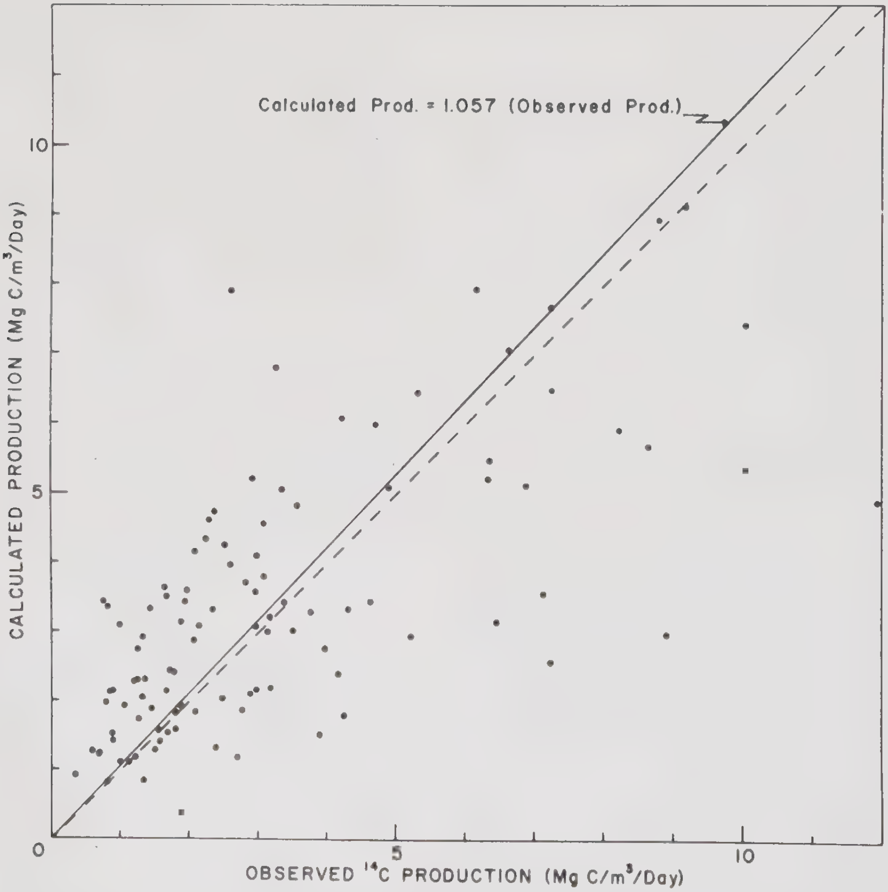

FIGURE 1.—Phytoplankton production calculated from ammonia and chlorophyll concentrations at 10 m compared with simulated *in situ* ^{14}C production at the 50 % light level in northerly nutrient-poor water in the eastern tropical Pacific Ocean. The dashed line is the regression that would be expected if agreement between the two sets of production values were perfect.

ammonium and where nitrate was undetectable. One hundred and five such production stations were available from 10 EASTROPAC cruises in this nutrient-poor water.

Production calculated from equation 3 is compared with measured ^{14}C production in Figure 1. There is a highly significant ($P<.01$) relationship between the two sets of values. The slope of the regression line is 1.057, which is very near to the value 1.0 which would be expected if agreement were perfect. Nevertheless, there is a large amount of scatter in the values of Figure 1; that is, the calculation overestimates in some cases and underestimates in others.

TABLE 2.—Errors in the calculation of production.

Parameter	Standard errors	Reference
Chlorophyll	± 12%	Holmes, Schaefer, and Shimada (1958)
R	± 17%	Eppley (1968)
μ_{max}	± 6%	Table 1 (this paper)
S	± 5%	Richards and Kletsch (1964)
K_s	± 76%	Table 1 (this paper)
Total	± 79%	
95% confidence limits	± 152%	

Errors in the values used in the calculation are given in Table 2. To figure total error these have been converted to variances and summed. The 95% confidence limit shows that any calculated production value can vary by ± 1.5 fold. Thus, one would expect quite a large scatter in Figure 1.

Most of the error is in K_s. When only the K_s values of Thomas (1970b) are used the calculation generally underestimates the observed ^{14}C production. Use of the mean of the K_s values of MacIsaac and Dugdale (1969) results in an overestimation. Since there is no reason to doubt either set of K_s values, we have used the overall mean K_s from Table 1. In applying this method to any other nutrient-limited waters, it would be well to obtain several values of K_s so that the error due to lack of precision in measuring K_s can be recognized.

Part of the scatter in Figure 1 may also be due to the fact that the parameter K_s is species—and temperature—dependent (Eppley, Rogers, and McCarthy, 1969) and that variations in species composition of the crop or slight variations in temperature may have affected the calculation. The parameters μ_{max} and R are also probably dependent upon the species composition of the crop and on temperature. Because of these factors, which are unknown, it is perhaps surprising that the relationship between calculated and observed production is so good when constant values of K_s, μ_{max}, and R are used.

This evidence supports the hypothesis that phytoplankton production in the upper mixed layer is controlled by the limiting nutrient, ammonium, and shows that the hyperbolic model describes this control very well. In this latter connection it should be noted that if a linear model having a term "S/S_{max}" in equation 3 (where S_{max} is that concentration supporting a maximum growth rate and which has a value near 10.0 μM from the data of Thomas, 1970b) is used rather than the term "$S/(K_s + S)$," the calculation very much underestimates the ^{14}C production. The linear model was used previously by Riley (1963) and Steele (1958) but should now be considered obsolete in view of more recent work using the hyperbolic model.

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Analysis of the Operations of Seven Hawaiian Skipjack Tuna Fishing Vessels, June-August 1967

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ABSTRACT

Analysis of operational data collected from seven Hawaiian skipjack tuna fishing vessels in the summer of 1967 showed that the vessels expended 38 percent of their day-baiting effort at Kaneohe Bay, which yielded 14.7 buckets of bait per set. Keehi Lagoon was, by far, the most productive night-baiting ground; it received 84 percent of the night effort and yielded 10.4 buckets per set.

On fishing trips which averaged 15.5 hours, 31 percent of the time was devoted to traveling to and from the fishing grounds, 62 percent was occupied by scouting, and only 7 percent was actually spent fishing. The vessels chummed 83 percent of the schools sighted, successfully fished 57 percent of the schools chummed, and used an average of 12.8 buckets of bait per trip. Most often seven men fished per school. Fishing duration among the vessels ranged from 1 to 155 minutes, but most schools were fished only for short periods.

Schools of large skipjack tuna (7 kg. or more), which dominate the summer catch, were usually fished further offshore.

About half of the schools sighted were in waters to the west of Oahu. Sightings increased from daybreak to a peak at 0801-0900, dipped at 1001-1100, then rose to a second peak at 1301-1400. The vessels caught 62 percent of their day's catch after 1200. Cloud cover and wave height at the time of fishing had no effect on the success or failure in fishing the school. Although the predominant species of bird associated with the school was not a good indicator of fishing success, size of the bird flock differed significantly among those schools with and without catches. Among schools yielding catches, the vessels found most associated with 50 or more birds; among those unsuccessfully fished, the vessels found most associated with 11-50 birds.

Data on support activities showed that it usually took nine men one-half hour to unload about 3.4 metric tons of skipjack tuna. The rate of unloading depended largely on the size of the fish. Loading ice required 6.6 minutes.

Comparison of data from high- and low-producing vessels showed that a high-producing vessel chummed the schools longer, used more bait in fishing, tended to remain with the school longer, and was successful in fishing a higher percentage of the schools it sighted.

INTRODUCTION

Since the early 1900's when the fishery for skipjack tuna, Katsuwonus pelamis, or aku, as it is locally called, began, the Hawaiian skipjack tuna fishermen have been modifying their vessels to increase their fishing power. They replaced scull or sail power with engines to increase the vessels' operating range, added a flying bridge to extend the vessels' scouting range, redesigned the hulls to improve the vessels' speed, stability, and maneuverability in rough channel waters around the islands, and increased the carrying capacities of the vessels' fuel tanks, ice holds, and baitwells.

The NMFS (National Marine Fisheries Service) (formerly the Bureau of Commercial Fisheries) in Honolulu also has attempted to improve fishing efficiency in the skipjack tuna fishery. Realizing that fishing with pole and line was often seriously hampered by a shortage of live bait, the NMFS tried purse seines (Murphy and Niska, 1953) and gill nets (Matsumoto, 1952; Shomura, 1963), but these attempts were unsuccessful in catching commercial quantities of skipjack tuna.

Until new means of catching skipjack tuna can be found, the Hawaiian tuna fishermen must rely on pole and line and live bait; therefore, the NMFS decided to try to improve the pole-and-line operation. This study of the operations of the fishery provides some basic information which is necessary for suggesting improvements. In addition, the information is potentially useful for obtaining the best possible index of abundance of the fish for biological studies.

SOURCE OF DATA

The captains and crewmembers of seven vessels participated in this study. NMFS technicians, who were permitted to remain aboard the vessels for 5-6 days a week, collected data on baiting, fishing, and supporting activities from June through August 1967.

When baiting, the technicians reported on the species and quantity caught, the mortality incurred in transporting the bait from catch site to the vessel, and the time required for the entire operation.

On fishing trips, the technicians recorded the time of departure and return and the start and end of scouting. For each school, they recorded the time of sighting, the start of chumming, and the start and end of fishing. They estimated the amount of bait used per school, noted the number of men that fished, counted the number of fish caught, and obtained the average weight of the fish in the school from a sample consisting of 10 fish selected at random. While pursuing the schools they estimated the amount of sky covered by clouds, the height of the waves, the number of birds in the flock, and identified the predominant birds associated with the school. After fishing and at 2-hour intervals while scouting, the technicians checked surface water temperatures and collected water samples for salinity determination. When possible, the technicians also approximated the positions of schools sighted and of schools fished by taking compass bearings from the vessel to recognizable landmarks. When landmarks were not visible, the captain estimated the position after considering the ship's course and approximate distance or hours from land.

In port, the technicians recorded time and number of men required to unload the catch and to load ice.

ANALYTICAL PROCEDURES

We summarized data on baiting, fishing, and supporting activities first by vessel, then collectively for all vessels over the 3 months. In examining the relation between any two variables, however, we separated the data into appropriate units, within which we summarized all other information important to our analysis. For example, in examining catch in relation to the number of men fishing, we separated the schools by number of men fishing; then, for each group (1, 2, 3,...10 men fishing) we summarized the catch per school and other information such as the amount of bait used and fishing duration.

We used data from incomplete logs in some of our analysis, but only after we established that the data would not bias the results. For example, on one vessel, a newly hired technician failed to record data on all schools sighted and chummed; therefore, his data were used only in summaries dealing with catch and not in summaries of schools sighted and chummed. The result was that although we could use the catch data from 244 trips, we were able to use the data on schools sightings from only 231 trips.

Catches of species other than skipjack tuna were infrequent (only about 0.8 percent, by weight); therefore, they were tabulated with the skipjack tuna catch. We considered that all fishing effort was expended with the primary purpose of catching skipjack tuna regardless of the species actually caught.

We agreed with the captains that the data collected would not be traceable to individual vessels so as to preserve anonymity; therefore we grouped the data or identified them with vessel code letters.

BAITING

The generalized block diagram in figure 1 shows the sequence of events which leads to a catch of skipjack tuna by a vessel. Basically, it begins with a period of baiting. (''Bait'' and ''baiting'' are colloquial terms which refer to the catching of bait.) Day baiting usually starts at dawn and ends when sufficient bait has been captured. If little or no bait is caught during the day, the vessel may attempt night baiting; if that proves unproductive, day baiting is resumed.

Within the Hawaiian Islands, there are several baiting grounds, but two of the major ones, which provide roughly two-thirds of the State's bait production (Yamashita, 1958), are on Oahu. There is Kaneohe Bay on the windward side of the island and Pearl Harbor on the leeward (fig. 2). A third site of some importance, particularly for night baiting, is Keehi Lagoon, also on the leeward side.

Having baiting grounds on windward and leeward Oahu has certain advantages. When fishing intensifies in windward Oahu waters, the vessels bait at Kaneohe Bay and return there after fishing to unload their catches, which are trucked to leeward Oahu where the markets and cannery are located. When fishing intensifies in leeward waters, the vessels bait at Pearl Harbor and at Keehi Lagoon and return after fishing to Kewalo Basin, home port of Oahu vessels and the site of the cannery.

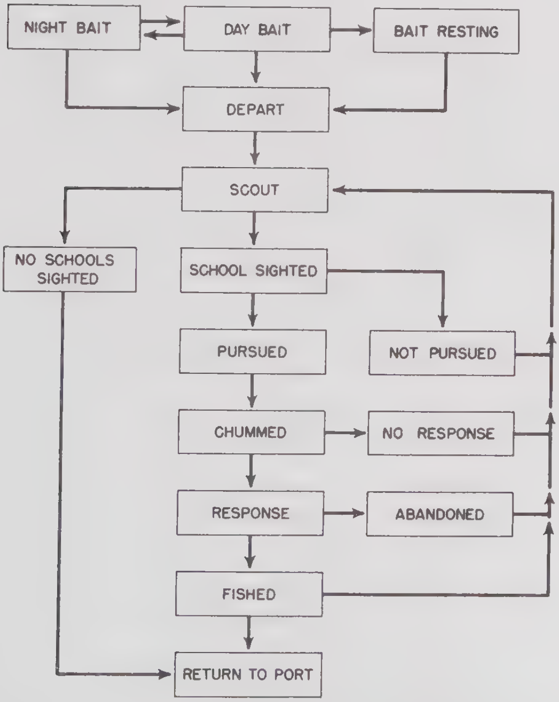

Figure 1.--Block diagram of baiting and fishing operation.

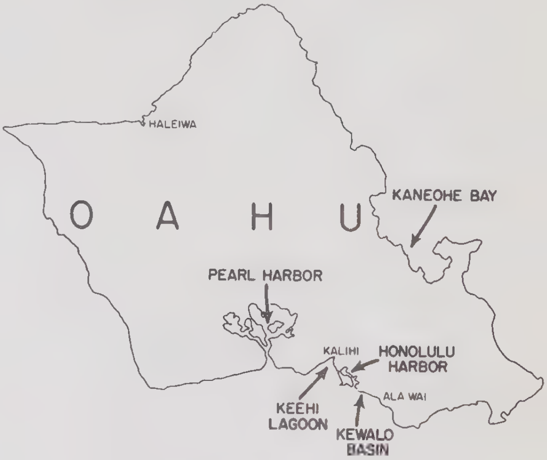

Figure 2.--Baiting areas on Oahu.

In 1948-66, bait production ranged from 23,622 to 49,712 buckets with an average of 36,465 buckets annually. Contributing 93 percent of the bait catch, the small (40-60 mm.), fragile Hawaiian anchovy locally called nehu, Stolephorus purpureus, is captured day and night and is the species preferred above all others by the skipjack tuna fishermen because it possesses most of the qualities of a good baitfish. Almost all the remainder of the bait catch is made up of silverside or iao, Pranesus insularum; other species sometimes used as bait constitute less than 1 percent of the bait catch.

Day Baiting

Day baiting, which usually begins at daybreak, frequently lasts for about 3 hours. The fishermen use an outboard skiff loaded with a surround net to scout for baitfish that school in shallow waters of bays and harbors or near river mouths. Having located a school, the fishermen surround it and then partially ''dry up'' the net to form a bag to hold the school. To avoid killing the bait,the fishermen ''swim'' the net-enclosed baitfish back to the vessel and transfer them into baitwells. Several sets may be required to obtain enough bait to justify fishing. We considered a set as a unit of baiting effort in this study. For additional information on baiting in Hawaiian waters, see June (1951).

Prior to 1968, Pearl Harbor was primarily a day-baiting ground for the Hawaiian tuna fleet. In June-August 1967, the seven vessels baited there 36 times and caught 1,093 buckets of bait in 108 sets or an average of 10.1 buckets per set (table 1). Mortalities at the time of capture were low, averaging 1.3 percent, and the amount released--either back into the water or transferred to another vessel because of an excess in catch--was 4.1 percent. Day baiting in Pearl Harbor usually lasted a little over 3 hours. Figure 3 shows that area 08, near the mouth of the Waiawa Stream in Middle Loch, was highly productive.

A ground for both a day and a night fishery for bait, Kaneohe Bay is usually the most productive baiting ground in the State. Catches in 41 days of baiting totaled 2,040 buckets of day bait in 139 sets or an average of 14.7 buckets per set, which is roughly 50 percent larger than the catch per set at Pearl Harbor (table 1). Mortalities, however, averaged about three times as much at Kaneohe Bay as at Pearl Harbor with roughly 3.8 percent of the total catch dead from various causes on the baiting grounds. The data also show that whereas bait released averaged 1.2 buckets for each day baited at Pearl Harbor, bait released at Kaneohe Bay averaged 3.9 buckets per day of baiting or roughly three times more than at Pearl Harbor. In time spent baiting, there appeared to be little difference between the two grounds. High producing areas in Kaneohe Bay can be seen in figure 3--area 47 off Waiahole and area 58 off Heeia had catches of 795 and 304 buckets, respectively.

Referred to frequently by the fishermen as ''Kalihi'' and understood to mean waters off the district of Kalihi in Honolulu, area 64 was the most productive in the Keehi Lagoon-Honolulu Harbor baiting grounds (fig. 3). Keehi Lagoon day bait catches--combined with those from Honolulu Harbor--totaled 506 buckets or about half the amount caught at Pearl Harbor (table 1). In 22 days of baiting, 51 sets yielded an average of 9.9 buckets per set or roughly the same amount per set as at Pearl Harbor. Baiting at Keehi Lagoon usually lasted a little longer than at any of the other baiting grounds for some unknown reason. Of the total bait caught,

Table 1.--Number of days or nights baited, catches, mortalities and releases, time spent baiting, and catch rates in baiting grounds fished by seven Hawaiian skipjack tuna vessels, June-August 1967

Baiting	Days baited	Bait transferred to well	Bait died	Bait released	Total catch	Total time	Mean baiting time	Catch per hour	Total sets	Catch per set	Catch per day	Catch per night
	Number	Bucket	Bucket	Bucket	Bucket	Minute	Minute	Bucket	Number	Bucket	Bucket	Bucket
Day:												
Pearl Harbor	36	1,034	14	45	1,093	5,870	190	11.2	108	10.1	30.4	-
Kaneohe Bay	41	1,803	77	160	2,040	7,868	192	15.6	139	14.7	49.8	-
Keehi Lagoon	22	457	13	36	506	4,427	201	6.8	51	9.9	23.0	-
Other areas	9	292	6	6	304	1,703	189	10.7	21	14.5	33.8	-
Total	108	-	-	-	3,943	-	-	-	319	12.4	36.5	-
Night:												
Kaneohe Bay	13	170	0	0	170	7,227	556	1.4	18	9.4	-	13.1
Keehi Lagoon	101	1,092	11	15	1,118	47,621	471	1.4	108	10.4	-	11.1
Other areas	3	24	0	0	24	1,220	407	1.2	3	8.0	-	8.0
Total	117	-	-	-	1,312	-	-	-	129	10.2	-	11.2

2.6 percent died at the baiting ground, whereas 7.1 percent were released. Areas 64-66 had good catches.

The vessels expended very little effort baiting at other areas such as Ala Wai and Haleiwa on Oahu and at grounds on neighboring islands. Nine days of baiting yielded 304 buckets in 21 sets or 14.5 buckets per set.

Collectively, the vessels had day catches totaling 3,943 buckets and averaging 36.5 buckets per day, enough to fill the baitwells on an average-sized vessel. In 319 sets or an average of 3.0 sets per day, the vessels averaged 12.4 buckets of bait per set.

Not all the bait caught reached the fishing grounds. The skipjack tuna catch reports of the Hawaii Division of Fish and Game show that about 25 percent of the bait die before use. We estimated that about 3 percent of the losses occurred on the baiting grounds during transport and transfer. The bulk of the losses, however, occurred between the time that the bait was safely aboard and arrival at the fishing grounds, but we are unable to give a reliable estimate of this loss because of insufficient data.

Night Baiting

In night baiting, there is no active scouting for schools of baitfish. Rather, a submerged light attracts the baitfish to the anchored or moored vessel. Usually just before daybreak, the fishermen set the net around the school and transfer the bait into the baitwells. So that they may have enough sleep, the fishermen rarely set the net more than once during the night. Night baiting frequently started at 1901-0100 and in 90 percent of the operations ended at 0501-0600; it usually lasted about 8 hours.

In recent years, the fishermen have found the baiting grounds at Keehi Lagoon (and Honolulu Harbor) very productive and attributed the good catches to increased nehu production in recently dredged areas. Actually, Keehi Lagoon accounted for only 16 percent of all day-baiting effort, but had 84 percent of all night-baiting effort, which totaled 129 sets. The reason is that until 1968, the U.S. Navy prohibited fishing

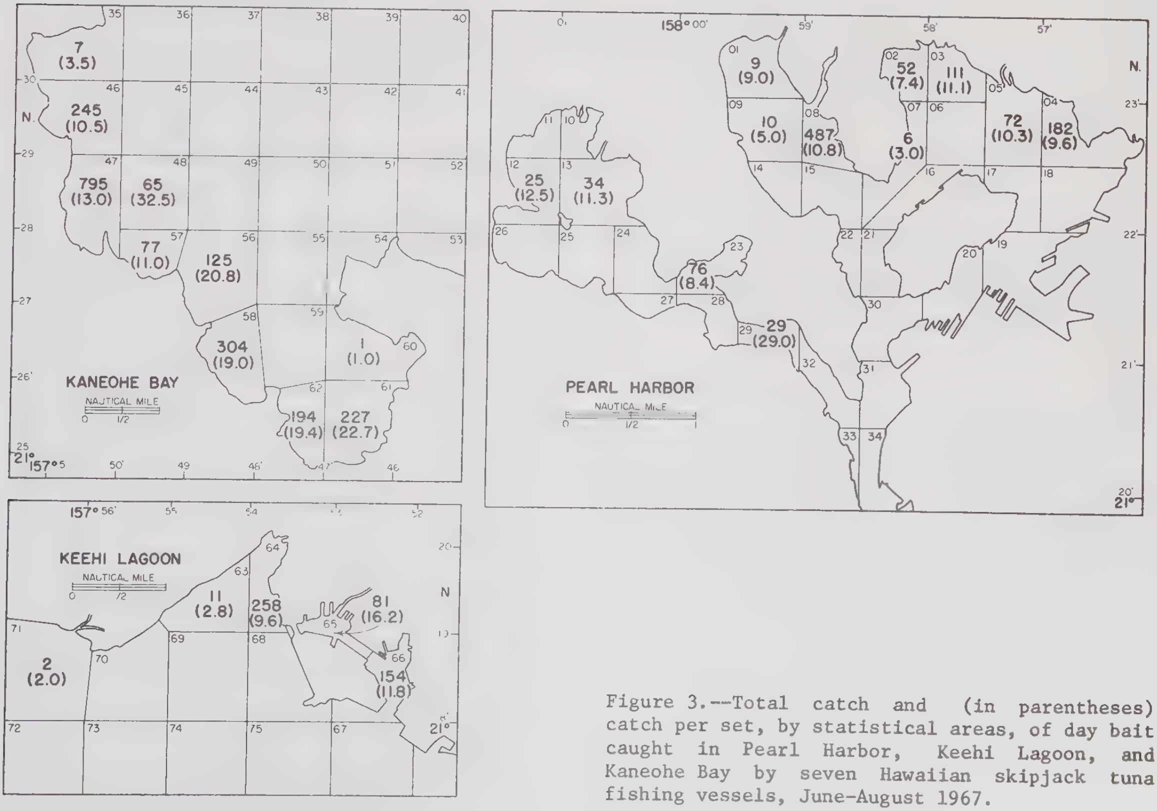

Figure 3.--Total catch and (in parentheses) catch per set, by statistical areas, of day bait caught in Pearl Harbor, Keehi Lagoon, and Kaneohe Bay by seven Hawaiian skipjack tuna fishing vessels, June-August 1967.

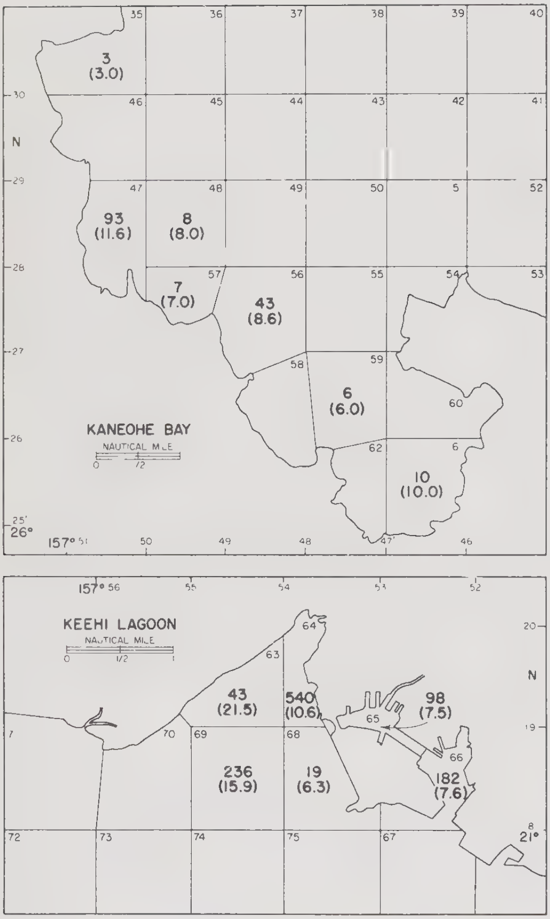

Figure 4.--Total catch and (in parentheses) catch per set, by statistical areas, of night bait caught in Kaneohe Bay and Keehi Lagoon by seven Hawaiian skipjack tuna fishing vessels, June-August 1967.

vessels from baiting at night at Pearl Harbor, the only other leeward baiting ground with any significant bait production. In 108 sets at Keehi Lagoon, the vessels caught 1,118 buckets or an average of 10.4 buckets per set (table 1). Figure 4 shows that areas 64 and 69 were highly productive night-baiting grounds.

The only other night-baiting ground of any importance was Kaneohe Bay. In 18 sets, the total catch reached 70 buckets or an average of 9.4 buckets per set (table 1). Like day baiting, night baiting was most productive in area 47 off Waiahole. The vessels spent only three nights catching bait from other baiting areas.

Collectively, in 117 nights of baiting, 129 sets produced 1,312 buckets of bait. Obviously, a few vessels made more than one set per night as evidenced by the difference in the number of nights baited and number of sets made. We calculated catch per set at 10.2 buckets, whereas catch per night reached 11.2 buckets. Frequently, catches of bait at night were insufficient for a day's fishing and the vessel spent additional time baiting during the day.

In night baiting, loss of bait through handling was minimal and amounted to less than 1 percent for all vessels over the 3-month period. Excess bait, which was released or shared with other vessels, amounted to about 1 percent of the total catch.

THE FISHING TRIP

The fishing trip starts only after sufficient bait is aboard to justify fishing. To be on the fishing grounds by sunrise, the fishermen usually restrict traveling to darkness, when they neither scout nor fish. From data on time of departure and return to port, we found that most trips originated between 0200 and 0600, with 41 percent originating at 0501-0600 (table 2). The vessels usually returned to port between 1800 and 2200, although there were a few trips that ended earlier or much later. Trips ending at 2001-2100 were most frequent (17 percent), but there were almost as many trips that ended at 1901-2000 (16 percent). By taking the difference in time between the length of the trip and the time expended in scouting and fishing, we calculated that traveling time on 231 trips averaged 4.8 hours or about 31 percent of an average trip of 15.5 hours. The average traveling time of individual vessels ranged widely from 3.6 to 6.5 hours per trip.

A fishing trip of a Hawaiian skipjack tuna vessel usually lasts 1 day, and has been used as the unit of effort in past studies on apparent abundance (Yamashita, 1958; Shippen, 1961; Uchida, 1966, 1967). In the section that follows, we discuss scouting, fishing, and catch per trip.

Scouting

Scouting, which averaged 9.7 hours or 62 percent of the time on an average fishing trip, is an essential part in fishing surface schools of tuna with either pole and line or purse seine and, therefore, is a major component of effort expended to catch fish. Usually, scouting started at daybreak; in 51 percent of the trips by 0600 and in 83 percent by 0700. On those trips where scouting started after 0700, the vessels usually spent part of the morning catching bait. Scouting continued until sunset, but rough weather, mechanical trouble, the need to unload the catch before spoilage, or the need to replenish the baitwells curtailed some trips. Scouting ended between 1700 and 1900 in 60 percent of the trips; most (36 percent) ended at 1801-1900.

Fishermen have long been aware of the association of sea birds with schools of fish. In Hawaii, the fishermen locate fish schools by relying almost exclusively on birds, large numbers of which flock and feed on prey driven to the surface by the skipjack tuna. Among the birds most frequently associated with fish schools are sooty tern, Sterna fuscata; noddy tern, Anous stolidus; wedge-tailed shearwater, Puffinus pacificus; and petrel, family Procellariidae, subfamily Hydrobatinae. In addition, other species which usually do not flock, but frequently associate with fish schools are the great frigate bird, Fregata minor; boobies, Sula spp.; and bo'sun (tropic birds), Phaethon spp.

In this report, we make the assumption that a fish school was associated with each bird flock sighted. This assumption appears justified. On two scouting cruises of the research vessel, Charles H. Gilbert, during the spring of 1953, Royce and Otsu (1955) found that "every one of 253 fish schools sighted was accompanied by birds and was found by means of birds." Although no mention is made of the number of flocks not associated with fish schools, we believe that most of the flocks sighted are associated with fish schools, because the fishermen can usually distinguish by observing the birds' behavior whether a school is nearby. Numbers of birds flying together in the same direction and not quartering back and forth or diving are usually regarded as scattered birds.

Bird flock sightings on 231 trips totaled 1,249 flocks or an average of 5.4 schools per trip. Vessel B, sighting 158 schools on 36 trips, averaged the least, with 4.4 schools per trip, whereas vessel E, sighting 320 schools on 51 trips, averaged the most, with 6.3 schools per trip (table 3). Trips with no sightings reached 2 percent. From the data in table 4 and figure 5, we found that 5 schools were sighted on one

Table 2.--Number and percentage of trips tabulated by time the vessels departed, started and ended scouting, and returned to port, Hawaii, June-August 1967

Time	Departure		Scouting started		Scouting ended		Returned to port	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
0001-0100	9	3.7	-	-	-	-	9	3.8
0101-0200	10	4.1	-	-	-	-	7	3.0
0201-0300	31	12.8	-	-	-	-	2	0.8
0301-0400	27	11.1	-	-	-	-	4	1.7
0401-0500	37	15.2	6	2.5	-	-	1	0.4
0501-0600	99	40.7	117	48.3	-	-	1	0.4
0601-0700	7	2.9	79	32.6	1	0.4	-	-
0701-0800	9	3.7	25	10.3	1	0.4	-	-
0801-0900	5	2.1	6	2.5	1	0.4	1	0.4
0901-1000	3	1.2	6	2.5	1	0.4	-	-
1001-1100	-	-	2	0.8	5	2.1	1	0.4
1101-1200	1	0.4	1	0.4	6	2.5	-	-
1201-1300	-	-	-	-	6	2.5	2	0.8
1301-1400	-	-	-	-	3	1.2	4	1.7
1401-1500	-	-	-	-	11	4.5	7	3.0
1501-1600	-	-	-	-	15	6.2	10	4.2
1601-1700	-	-	-	-	20	8.2	10	4.2
1701-1800	-	-	-	-	56	23.1	9	3.8
1801-1900	-	-	-	-	78	36.4	28	11.9
1901-2000	-	-	-	-	28	11.6	38	16.1
2001-2100	3	1.2	-	-	-	-	40	17.0
2101-2200	-	-	-	-	-	-	29	12.3
2201-2300	2	0.8	-	-	-	-	23	9.8
2301-2400	-	-	-	-	-	-	10	4.2
Totals	243	-	242	-	242	-	236	-

out of five trips, that from one to five sightings were reported on more than half of the trips (57 percent), and that 18 schools were the most sighted on one trip.

When a flock is sighted, the vessel pursues it in an attempt to head off the school and begin chumming. The interval between sighting and the start of chumming, which we called pursuit time, varied widely among the vessels. Considered an integral part of scouting time because scouting continues even when the vessel is pursuing a school, pursuit time is obviously influenced by the vessel's speed and its distance from the school at the time of sighting. Some elements, however, prolong pursuit time; for example, when schools are scarce on the fishing grounds, a captain may feel compelled to chase a nonbiting school longer than usual, or to drift and wait up to an hour for schools that have sounded to return to the surface.

The frequency distribution of pursuit time, tabulated by 5-minute intervals, was strongly skewed toward short intervals (table 5 and fig. 6). Pursuit time ranged from 1 to 105 minutes, but the mode in the distribution occurred at 6-10 minutes. The vessels pursued about 80 percent of the schools for 20 minutes or less, 15 percent from 21 to 40 minutes, and 5 percent longer than 40 minutes. Among the vessels, pursuit time averaged from 9.4 minutes for vessel G to 31.5 minutes for vessel C with a grand mean of 15.0 minutes (table 3).

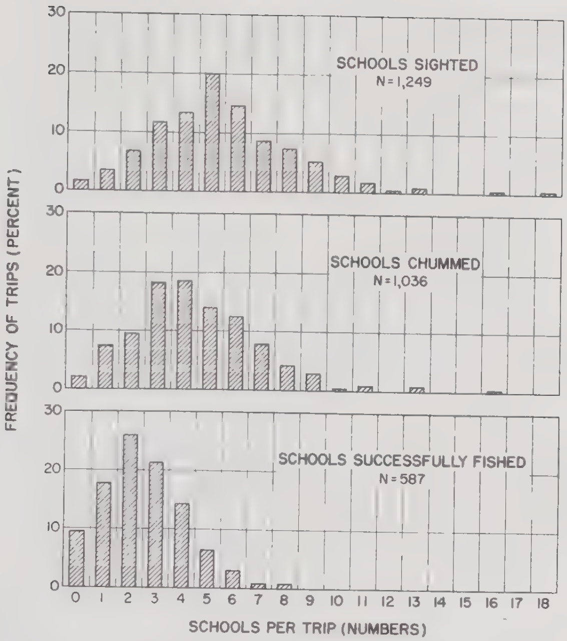

Figure 5.--Percentage frequency of trips tabulated by the number of schools sighted, chummed, and successfully fished per trip by seven Hawaiian skipjack tuna fishing vessels, June-August 1967.

Table 5.--Number, percentage, and cumulative percentage frequencies of schools pursued and chummed by seven Hawaiian skipjack tuna fishing vessels, tabulated by pursuit and chumming time in 5-minute intervals, June-August 1967

Time	Pursuit time			Chumming time		
Minute	Number	Percent	Cumulative percent	Number	Percent	Cumulative percent
<1	-	-	-	25	4.1	4.1
1-5	228	22.2	22.2	357	58.1	62.2
6-10	254	24.7	46.9	81	13.2	75.4
11-15	217	21.1	68.0	47	7.6	83.0
16-20	117	11.4	79.4	22	3.6	86.6
21-25	64	6.2	85.6	22	3.6	90.2
26-30	56	5.4	91.0	19	3.1	93.3
31-35	25	2.4	93.4	9	1.5	94.8
36-40	10	1.0	94.4	14	2.3	97.1
41-45	14	1.4	95.8	5	0.8	97.9
46-50	7	0.7	96.5	4	0.6	98.5
51-55	5	0.5	97.0	1	0.2	98.7
56-60	9	0.9	97.9	-	-	-
>60	21	2.1	100.0	8	1.3	100.0
Totals	1,027	-	-	614	-	-

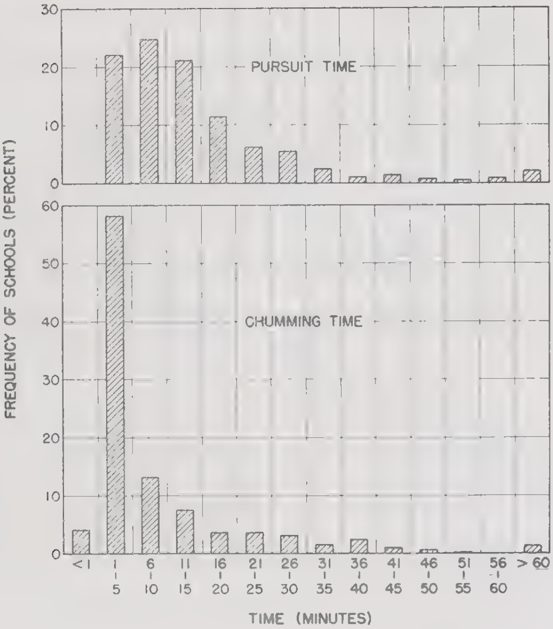

Figure 6.--Frequency of pursuit time and chumming time per school for seven Hawaiian skipjack tuna fishing vessels, June-August 1967.

Chumming starts as soon as the vessel crosses the head of the school and if the fish start to bite, the chummer throws more bait to bring the school near the stern so fishing can start. If there is no response, chumming stops temporarily, marking the completion of a "pass." Usually, then, the vessel is swung around for another pass. We defined chumming time as the interval from the start of chumming to the landing of the first fish and calculated it only for those schools with catches because we did not record the time that a nonresponsive school was abandoned.

The distribution of chumming time, which varied from less than a minute to 141 minutes, was strongly skewed; chumming lasted less than a minute in 4 percent of the schools, 1-5 minutes in 58 percent, 6-10 minutes in 13 percent, and 11 minutes or more in 25 percent (table 5 and fig. 6). Chumming time, which varied widely, reflects the biting behavior of schools; some bit readily, whereas others responded slowly. Vessel F chummed an average of only 4.6 minutes per school, the least among the vessels; it probably abandoned nonresponsive schools early (table 3). Vessel E chummed the longest, spending an average of 13.2 minutes per school before catching any fish. Chumming time of all vessels averaged 9.4 minutes per school.

We estimated that collectively on 231 trips the vessels chummed 1,036 schools out of 1,249 schools sighted or about 83 percent. Table 4 and figure 5 show that the distribution of trips, tabulated by the number of schools chummed, was moderately skewed, that the number of schools chummed per trip ranged from 1 to 16, and that trips on which the vessels chummed three or four schools were most frequent. Reference to individual vessels showed that the percentage of schools chummed varied widely from 66 percent for vessel C to 97 percent for vessel G, which incidentally chummed 5.4 schools per trip, the highest average among the vessels. Vessels B and C, both with the lowest rates, averaged 3.8 schools per trip. The grand mean was 4.5 schools per trip (table 3).

Sometimes, a vessel will pass up a school or abandon one even before catching fish. There were 653 schools which were not fished for reasons given in table 6. About half of the schools did not respond to chum and were abandoned, 28 percent sounded or moved too fast to overtake, 18 percent were composed of fish too small for canning or marketing, and 4 percent were passed up so that the vessels could fish other schools.

Table 6.--Number and percentage of 653 schools not fished by the seven Hawaiian skipjack tuna fishing vessels, tabulated by their reasons for abandoning the schools, June-August 1967

Reasons for not fishing	Schools	
	Number	Percent
Chummed but no response	322	49.3
School sounded or moving too fast	182	27.9
Fish too small	120	18.4
Chummed another school close by	29	4.4

Fishing

In fishing skipjack tuna schools with pole and line and live bait, the vessels usually fish only a few minutes and catch a variable fraction of the fish from each school. Fishing time per trip, the sum of the time spent fishing each school, averaged 68 minutes (1.1 hours), which is only about 7 percent of the average trip time. There was, however, a wide variation--

from 46 to 96 minutes--in the average fishing time per trip of the vessels.

The catch from a skipjack tuna school is the outcome of complex and interacting components. For example, the fishermen can control the number of men fishing and to some degree have control over fishing duration, the amount of bait used, and size of fish they will catch, but have no control over the school's biting behavior which adds to the complexity of producing a catch. Furthermore, skill and experience of crewmembers are part of this complex system, but these components are difficult or impossible to quantify.

In Hawaiian waters, the probability that a vessel will catch one or more fish from a school is roughly 50 percent. Royce and Otsu (1955), who examined scouting data over a period of 10 months, reported 43 percent success, whereas Yuen (1959), who had data for the fishing season from May to September, reported 48 percent success among the schools chummed. Collected at the peak of the fishing season in June-August, our data showed that the vessels chummed 1,036 schools (August data for vessel F not included) and caught one or more fish from 587 schools or 57 percent. Individually, vessel A was most successful, fishing 68 percent of the schools it chummed; vessel B was least successful, fishing only 48 percent. In the section that follows, we discuss various components as they relate to fishing.

Amount of bait used.--The amount of bait caught or used in the fishery is measured in units of a "bucket," which holds varying amounts of bait, but usually about 3.6 kg. In the beginning, we attempted to keep an accurate, daily record of the quantity of bait in each baitwell and the subsequent rate at which that bait was used or died at sea, but found the procedure impractical on commercial fishing vessels. We did, however, obtain data on amount of bait used on each school, some of which required more than a bucket, others less. We used one bucket as a minimum, even though on some schools only a few handfuls or some fraction of a bucket were used in chumming. The amount of bait used, therefore, may be overestimated, but we believe any error to be reasonably small.

We compared our estimate of bait used per trip, which averaged 12.8 buckets (table 3), and an earlier estimate made by Uchida (1967) and found them similar. Uchida showed that in 1952-62, small vessels used 12.3 buckets and large vessels used 15.4 buckets of bait per trip, whereas our data showed that, individually, the

Table 7.--Number of schools with and without catches, and averages of catch per school, number of men fishing per school, fishing duration per school, and size of fish per school, tabulated by the amount of bait used per school by seven Hawaiian skipjack tuna vessels, June-August 1967

Bait used per school	Schools		Catch per school		Men fishing	Fishing duration	Fish size
	With catches	Without catches					
Bucket	Number	Number	Number	Metric ton	Number	Minute	Kg.
1	108	383	42.0	0.1	6.1	8.6	3.4
2	111	18	81.6	0.4	6.9	15.3	5.4
3	99	8	110.8	0.7	6.8	21.0	6.6
4	75	1	158.0	1.1	6.7	25.4	6.7
5	76	3	164.6	1.2	6.8	30.3	7.6
6	43	-	203.6	1.7	6.8	37.5	8.2
7	26	-	205.8	1.8	7.5	41.1	8.8
8	27	-	187.4	2.0	7.3	44.8	10.9
9	8	-	259.9	3.0	7.4	53.6	11.4
10	18	-	251.9	2.3	6.9	53.0	9.2
11	4	-	771.8	1.8	7.5	93.2	2.3
12	8	-	680.8	3.3	8.0	66.6	4.9
13	6	-	421.2	4.4	7.8	69.7	10.4
14	2	-	323.0	3.7	8.0	92.5	11.5
15	4	-	433.8	5.2	8.0	72.0	12.0
>15	7	-	583.7	5.0	7.8	98.3	8.5

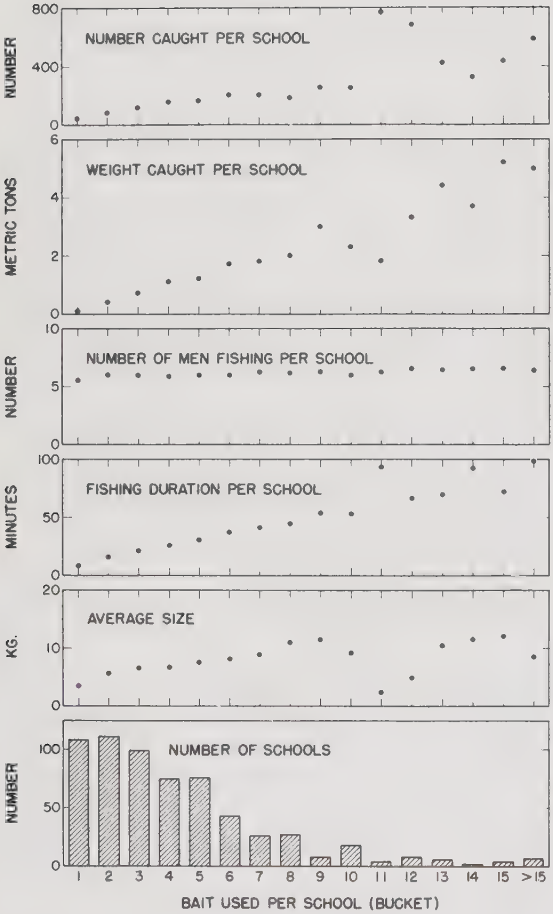

Figure 7.--Relation between amount of bait used per school and average values of catch per school, number of men fishing per school, fishing duration per school, and size of fish per school, June-August 1967.

vessels used from 9.0 to 22.6 buckets per trip. Fully loaded, most vessels carry at least 36 buckets of bait, and sometimes much more, per trip.

A vessel with a full load of bait can fish 2-3 days, provided the bait does not die or is not used up rapidly because of good fishing. That chummers generally used bait sparingly is reflected in the data in table 7, which shows that among nonresponding schools, the vessels chummed 93 percent with only one bucket and the remainder usually with two to five buckets of bait. Even among responding schools, the vessels fished 75 percent with up to only five buckets of bait (table 7 and fig. 7). The average amount of bait used per school, by vessel, ranged from 2.1 to 5.0 buckets per school. Collectively, the average was 3.0 buckets per school (table 3).

Figure 7 shows the averages of the catch per school, number of men fishing, fishing duration, and fish size, plotted by the amount of bait used per school. To show the mutual relationship between the variables examined, we calculated and tested the correlation coefficients, using a hypothesis of $\rho = 0$. We found all the correlation coefficients differing significantly from the hypothesis (table 8). We concluded that the amount of bait used, therefore, contributed significantly to the average number and weight of fish caught per school. It is also evident that on schools requiring more bait, the average fish size was larger and fishing duration longer. Usually, more men fished those schools that required more bait.

To measure the fleet's efficiency in the production of skipjack tuna relative to the bait supply, two indices are occasionally used--catch per bucket of bait caught and catch per bucket of bait used (Yamashita, 1958; Brock and Uchida, 1968). Because we did not collect data for all baiting and fishing operations, we could not calculate the catch per bucket of bait caught; instead, we calculated the catch per

Table 8.--The correlation coefficients calculated for the relation between bait used, men fishing, fishing duration, and fish size and the averages per school of the number and weight of fish caught, amount of bait used, men fishing, fishing duration, and fish size. A single asterisk denotes probabilities between 0.05 and 0.01; two asterisks denote probabilities equal to or less than 0.01

Components of catch	Bait used	Men fishing	Fishing duration	Fish size
Number caught	0.744**	0.956**	0.979**	-0.456
Weight caught	0.939**	0.940**	0.960**	0.852**
Bait used	-	0.977**	0.946**	0.813**
Men fishing	0.899**	-	0.753**	0.300
Fishing duration	0.934**	0.822**	-	0.592*
Fish size	0.510*	0.705	0.847**	-
Degrees of freedom	13	6	10	10

bucket of bait used (table 3). We found that a high-producing vessel does not necessarily have the highest catch rate per bucket of bait used. Vessel A, which ranked first in catch per trip with 4.1 metric tons and third in catch per school with 1.3 metric tons, ranked sixth with a catch of 179.3 kg. per bucket of bait used, whereas vessel F, which ranked lowest in both catch per trip with 2.0 metric tons and catch per school with 0.7 metric ton, ranked fourth or better than average with a catch of 225.3 kg. per bucket of bait used. The averages of the other vessels varied from 174.6 to 262.0 kg.

Number of men fishing.--In pole-and-line fishing, each fisherman uses a stout bamboo pole with a line and a lure consisting of a barbless hook to which feathers and a soft, plastic skirt are attached. Simulating a live baitfish, the lure is slapped on the water and moved over the surface, which is rippled by water sprays from the vessel to enhance the feeding frenzy. When a fish strikes, the fisherman quickly leans back on the pole, taking advantage of the fish's initial thrust to lift it out of the water and "flip" it onto the deck in one continuous motion. By relaxing the tension on the pole, the fisherman allows the fish to become unhooked then returns the freed hook to the water.

On Hawaiian vessels, the "good hookers" fish at the stern where fishing is usually best while others fish along the gunwales near the stern. Every crewmember fishes except the chummer. On some vessels, however, the captain, engineer, and perhaps one fisherman fish only intermittently so they were counted as fishing only if they fished more than half of the fishing duration.

Although the number of men fishing per school ranged from 1 to 10, it was very unusual to have fewer than 3 men fishing (table 9). All the fishermen may not be in their positions at the stern when the school starts biting; those who are may catch a few fish before biting stops. In counting the number of men fishing, we included only those fishermen in position at the time of fishing. Usually, between six and eight men fished; most often, there were seven men fishing (fig. 8).

Catch increased as the number of men fishing increased, but not proportionally. For example, table 9 shows that four men caught an average of 0.4 metric ton, whereas eight men averaged 1.3 metric tons or about three times as much. Plots of the data in table 9 showed positive upward trends of all the variables as the number of men hooking increased; all except one of the correlation coefficients differed significantly when tested against the hypothesis $\rho = 0$ (table 8). The exception was that for the correlation between fish size and number of men fishing. The test of the coefficient against the hypothesis showed a probability very close to 0.05, the level of rejection; however, we accepted the hypothesis on the basis of the summary, by fish size, to be presented in a later section. We conclude from our tests that when the vessels made large catches, they usually had more men fishing, used more bait, and fished the schools longer.

Table 9.--Number of schools and averages of catch per school, amount of bait used per school, fishing duration, and fish size, tabulated by the number of men fishing per school on seven Hawaiian skipjack tuna vessels, June-August 1967

Men fishing per school	Schools	Catch per school		Bait used per school	Fishing duration	Fish size
Number	Number	Number	Metric ton	Bucket	Minute	Kg.
1	4	1.0	<0.1	1.5	5.0	10.0
2	–	–	–	–	–	–
3	7	8.1	<0.1	1.0	3.3	3.3
4	16	76.3	0.4	2.1	11.2	5.7
5	64	109.9	1.0	3.8	22.3	9.0
6	152	140.0	0.9	3.8	27.4	6.3
7	188	143.2	1.1	4.2	27.8	7.6
8	138	180.2	1.3	5.0	29.1	7.0
9	41	194.4	1.6	5.9	32.2	8.4
10	9	306.7	2.6	7.3	29.4	8.5

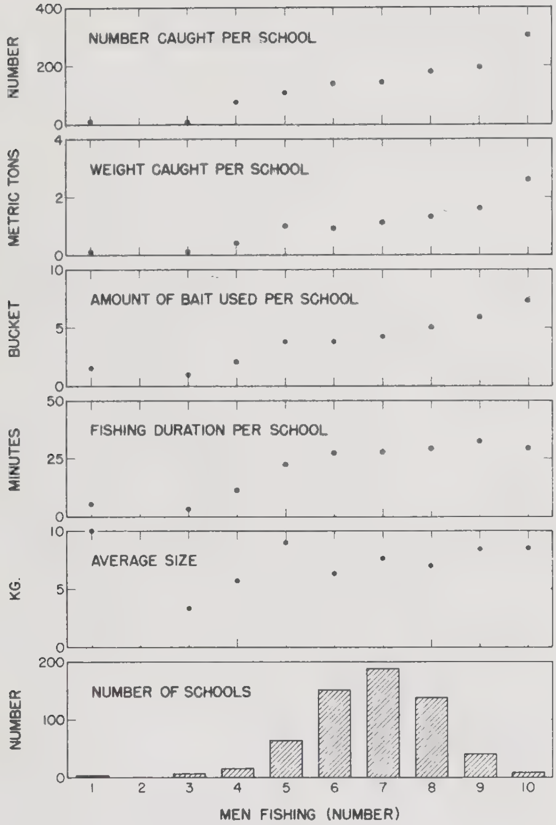

Figure 8.--Relation between number of men fishing per school and average values of catch per school, amount of bait used per school, fishing duration per school, and size of fish per school, June-August 1967.

Fishing duration.--Fishing ends either when the captain decides to abandon the school or when the school breaks away from the vessel. We defined fishing duration as the elapsed time from the landing of the first fish to the end of fishing and for 617 schools found that, although ranging widely from 1 to 155 minutes, it was usually short. The distribution of fishing duration (table 10 and fig. 9), grouped into 5-minute intervals, peaked at 6-10 minutes, with progressively fewer schools fished at longer durations.

Biting behavior has a strong influence on fishing duration. The captains abandoned 42 percent of the schools after fishing started, because biting slowed to a point where they could no longer justify further expenditure of time and live bait (table 11). Moreover, they abandoned an almost equally large percentage--40 percent--of the schools after biting stopped, whereas they abandoned only 8 percent because the schools sounded and failed to return to the surface. In the remaining 11 percent of the schools, the captains quit fishing when they learned that the schools consisted of small fish, when predators--shark or billfish--attacked and dispersed the school, or when bait was exhausted.

It follows that biting behavior influences not only fishing duration, but also the amount of bait chummed to hold the school near the vessel and the catch. Table 10 and figure 9 show that the vessels usually used more bait and caught more fish from good-biting schools that

Table 10.--Number of schools and averages of catch per school, amount of bait used per school, number of men hooking per school, and fish size, tabulated by fishing duration per school for seven Hawaiian skipjack tuna vessels, June-August 1967

Fishing duration	Schools	Catch per school		Bait used per school	Men hooking	Fish size
Minute	Number	Number	Metric ton	Bucket	Number	Kg.
1-5	63	29.3	0.1	1.5	6.2	3.2
6-10	88	62.3	0.3	2.1	6.6	4.2
11-15	82	106.7	0.5	2.7	6.9	4.7
16-20	70	122.0	0.8	3.5	6.9	6.9
21-25	68	140.0	0.9	3.8	6.8	6.4
26-30	59	151.1	1.3	4.9	6.9	8.5
31-35	39	187.8	1.4	5.2	6.7	7.6
36-40	37	220.7	1.9	5.7	6.9	8.7
41-45	20	222.1	2.3	6.8	6.9	10.5
46-50	17	204.9	1.7	5.7	6.8	8.2
51-55	11	257.6	2.5	8.3	7.1	9.8
56-60	11	277.7	2.2	6.4	7.3	7.9
>60	52	379.8	2.9	10.4	7.3	7.8

stayed with the vessel longer. Excluding fishing duration of longer than 60 minutes, we calculated correlation coefficients for the data in table 10 and found that they differed significantly from $\rho = 0$. Figure 9 shows that the average number and weight of fish caught per school were larger with more time spent fishing the schools. It also turned out that the vessels usually had more men fishing those schools that bit longer, possibly because the captains and engineers spent more time fishing and were, therefore, included in the effort. Our data showed that the vessels usually caught larger fish from schools that bit longer.

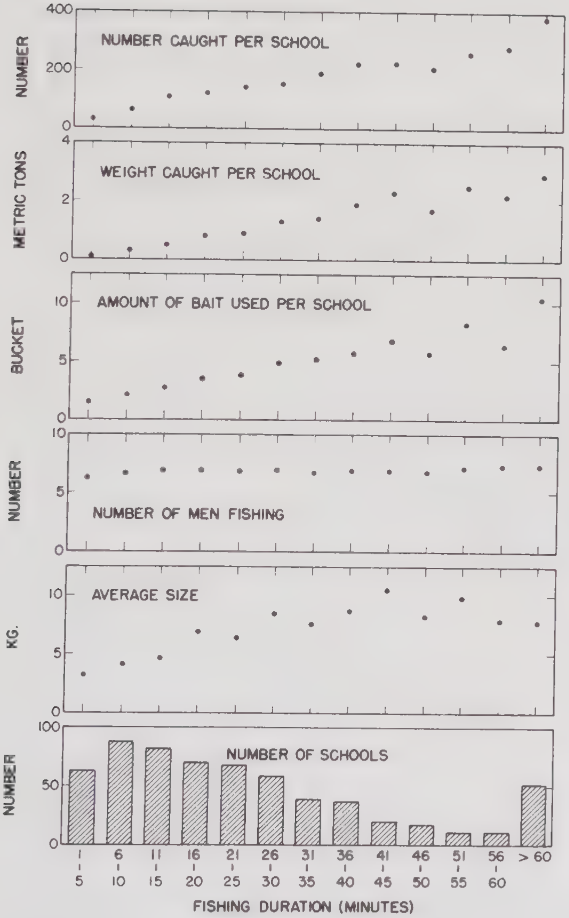

Figure 9.--Relation between fishing duration and average values of catch per school, amount of bait used per school, number of men fishing per school, and size of fish per school, June-August 1967.

Table 11.--Number and percentage of 585 schools fished by seven Hawaiian skipjack tuna fishing vessels, tabulated by reasons cited for abandoning successfully fished schools, June-August 1967

Reason for abandoning schools	Schools	
	Number	Percent
Biting slowed	244	41.7
Biting stopped	232	39.6
School sounded	46	7.9
Other reasons (small fish, presence of predators, no bait left)	63	10.8

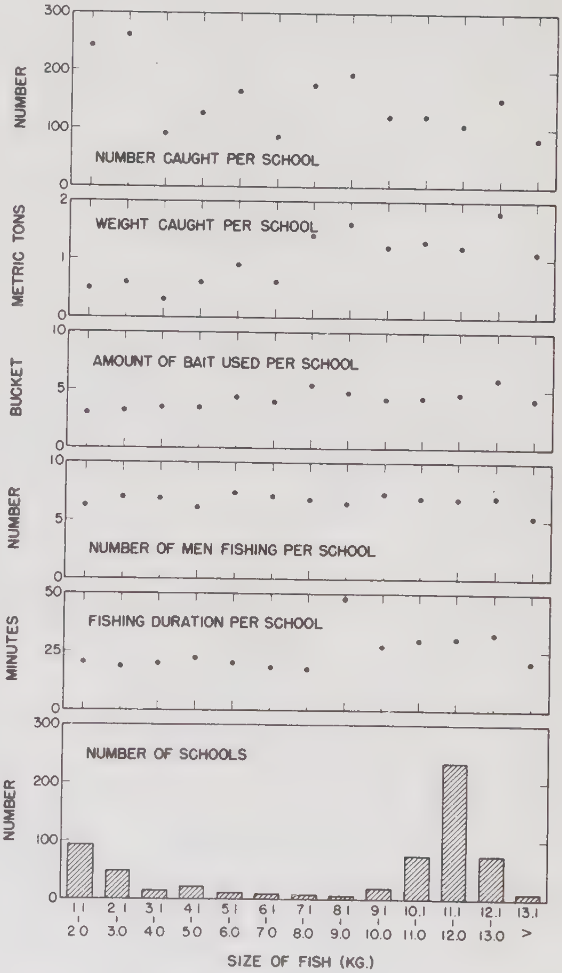

Figure 10.--Relation between size of fish and average values of catch per school, amount of bait used per school, number of men fishing per school, and fishing duration per school, June-August 1967.

Table 12.--Number of schools and averages of catch per school, amount of bait used per school, number of men fishing per school, and fishing duration per school, tabulated by size of fish caught by seven Hawaiian skipjack tuna vessels, June-August 1967

Fish size	Schools	Catch per school		Bait used	Men fishing	Fishing duration
Kg.	Number	Number	Metric ton	Bucket	Number	Minute
1.1-2.0	93	242.4	0.5	3.0	6.3	20.5
2.1-3.0	49	261.9	0.6	3.2	7.0	18.5
3.1-4.0	15	91.3	0.3	3.5	6.9	19.8
4.1-5.0	22	122.7	0.6	3.5	6.1	22.1
5.1-6.0	11	164.3	0.9	4.4	7.4	20.0
6.1-7.0	9	85.1	0.6	4.0	7.1	18.0
7.1-8.0	8	173.8	1.4	5.4	6.8	17.5
8.1-9.0	6	192.3	1.6	4.8	6.5	47.7
9.1-10.0	19	120.4	1.2	4.2	7.3	27.1
10.1-11.0	74	121.0	1.3	4.3	6.9	29.6
11.1-12.0	233	105.2	1.2	4.6	6.8	30.4
12.1-13.0	74	149.9	1.8	5.9	7.0	32.3
>13.0	10	81.7	1.1	4.2	5.3	20.2

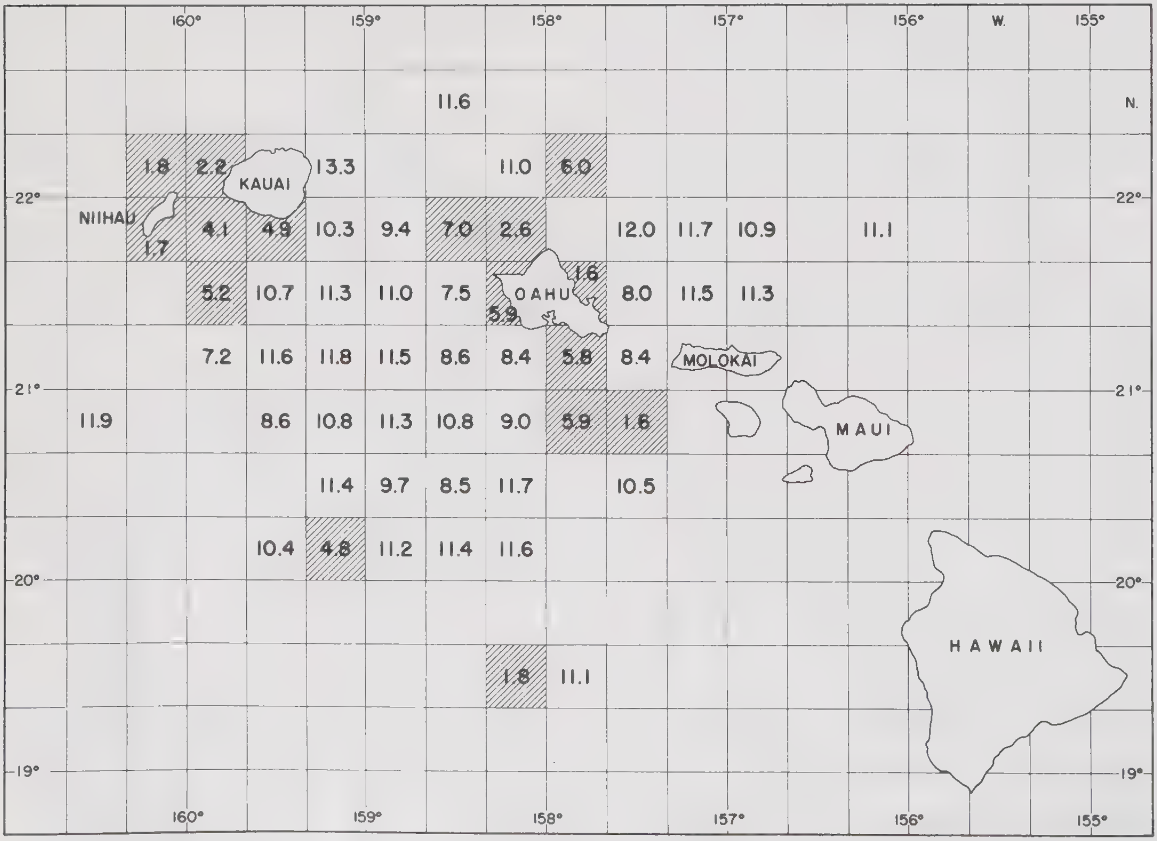
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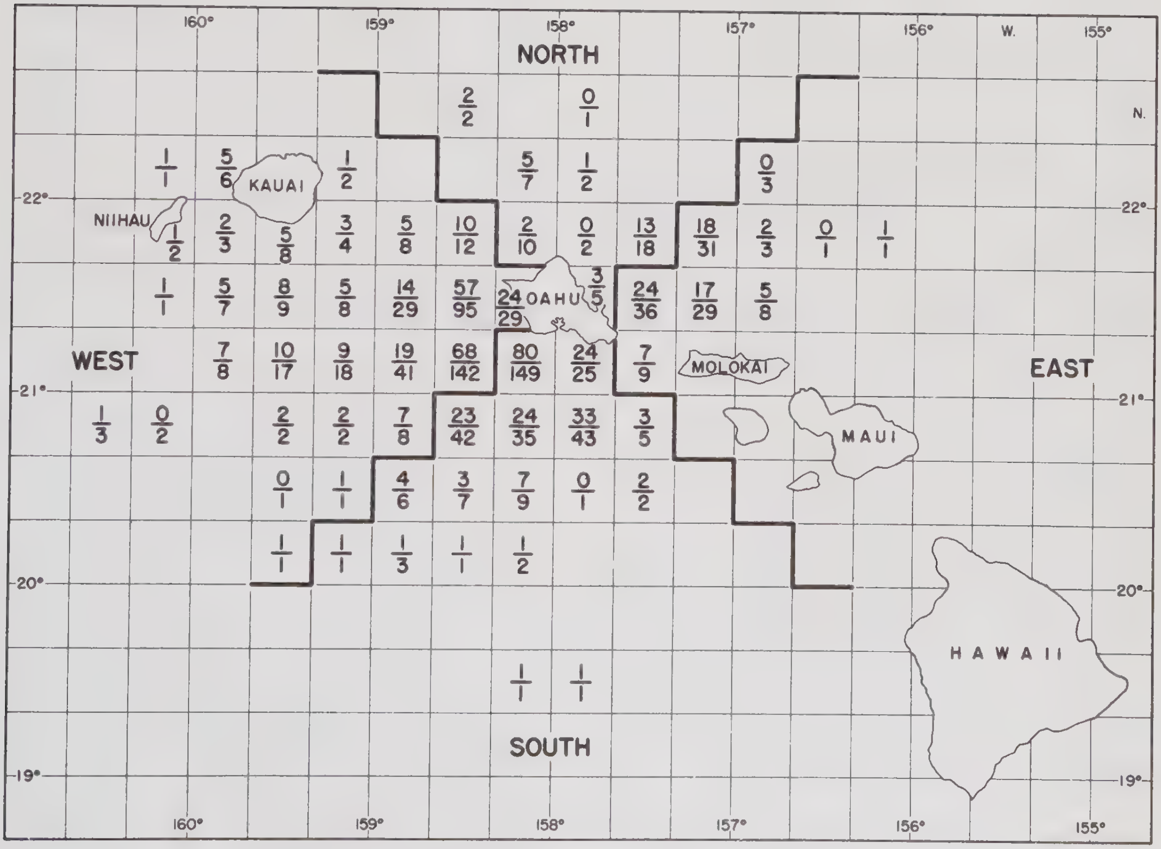
Figure 11.--Average size (kg.) of skipjack tuna caught in 20-minute areas of longitude and latitude by seven Hawaiian skipjack tuna fishing vessels, June-August 1967. Areas in which skipjack averaged 7 kg. or less are shaded.

Size of fish.--The size of skipjack tuna caught in Hawaiian waters is an important factor in the success of a fishing season. The influx of large numbers of "season" fish in the fishery marks the height of the fishing season, usually from May to September, and these fish constitute a major portion of the landings annually.

There appear to be four size groups in the catch: < 4 kg. = small; 4-7 kg. = medium; 7-10 kg. = season; and > 10 kg. = extra large. Because large fish bring better prices, the Hawaiian tuna fishermen usually pass up schools of small and sometimes medium fish for large "season" fish. In table 12 and figure 10, which show the size of fish caught by the seven vessels in June-August 1967, we noted that "season" fish were rather scarce in the catch, constituting only about 5 percent of the schools fished. Much more frequent were schools of extra-large fish (63 percent), which are usually not as frequently encountered as schools of "season" fish, and schools of small fish (25 percent), with schools of medium fish only slightly more frequent in the catch than schools of "season" fish. We also plotted the averages of catch per school, amount of bait used per school, number of men hooking per school, and fishing duration, by fish size, and found that some tended to increase whereas one decreased as fish size increased; only two of the correlations, those for the number of fish caught per school and for the number of men fishing per school with size of fish, did not differ significantly (table 8). The fact that the correlation coefficient of the average number of men fishing and fish size did not differ significantly led us to our earlier conclusion that variation in the number of men fishing did not contribute to variation in average fish size.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155°

Figure 12.--Ratio of the number of schools successfully fished (upper figure) to the number of schools sighted (lower figure), by 20-minute areas of longitude and latitude in Hawaiian waters, June-August 1967.

A plot of fish size by area of catch showed that larger fish were usually caught farther offshore. Separating the fish sizes into two categories, we found fish averaging smaller than 7 kg. concentrated in six 20-minute areas near Niihau and Kauai, in eight areas around Oahu, and in only two isolated, offshore 20-minute areas south of Kauai and Oahu (fig. 11). Most of the areas with fish averaging larger than 7 kg. were far offshore.

Spatial and temporal distributions of sightings and catches.--The vessels, concentrating their fishing in those areas where skipjack tuna showed the greatest tendency to aggregate in the past, obtain a major portion of the skipjack tuna catch each year from waters to the southwest of Oahu. Commonly called "shitaba" (which means lower ground in Japanese) by the fishermen, this leeward fishing ground off Oahu is calm almost year-round and close to the home port of Oahu-based vessels as well as to Pearl Harbor, one of two major baiting grounds in the Hawaiian Islands. We arbitrarily divided the fishing grounds around Oahu into four sectors and found that out of 971 sightings for which positions were recorded, nearly half were in waters to the west of Oahu, 34 percent to the south, about 13 percent to the east, particularly north of Molokai, and only 5 percent to the north (fig. 12).

Sightings varied not only by geographic location, but also by time of day. The number of sightings in relation to time of day increased rapidly from daybreak to a peak at midmorning (0801-0900), followed by a slight dip at 1001-1100 and a second peak at 1301-1400 (table 13 and fig. 13). We believe that reduced scouting intensity during mealtimes may have caused the slight dip at midday. Data on mealtime aboard the seven vessels showed that on nearly half of the trips, the crewmembers ate lunch at 1001-1100, which coincided with the slump in sightings (table 14). Undoubtedly, insufficient light and scarcity of birds at 0501-0600 and at 1801-1900 affected sightings, but the time taken for breakfast and dinner also may have had some effect on scouting intensity.

Data collected during a research cruise of the Charles H. Gilbert in April 1953 showed similar variations in sightings, by time of day (Royce and Otsu, 1955). Sightings, recorded by fishermen maintaining a continuous watch, dipped at midday and peaked at 0700-0800 and at 1400-1600. Royce and Otsu stated that there

Table 13.--Number and percentage of schools sighted and of schools with catches, tabulated by time of sighting and start of fishing, for seven Hawaiian skipjack tuna vessels, June-August 1967

Time	Schools			
	Sighted		With catches	
	Number	Percent	Number	Percent
0001-0100	-	-	-	-
0101-0200	-	-	-	-
0201-0300	-	-	-	-
0301-0400	-	-	-	-
0401-0500	-	-	-	-
0501-0600	11	0.9	1	0.2
0601-0700	60	4.7	21	3.4
0701-0800	119	9.4	36	5.8
0801-0900	144	11.3	66	10.6
0901-1000	130	10.2	67	10.8
1001-1100	112	8.8	50	8.1
1101-1200	121	9.5	60	9.7
1201-1300	122	9.6	70	11.3
1301-1400	124	9.8	56	9.0
1401-1500	91	7.2	62	10.0
1501-1600	97	7.6	46	7.4
1601-1700	72	5.7	42	6.8
1701-1800	52	4.1	26	4.2
1801-1900	16	1.2	17	2.7
1901-2000	-	-	-	-
2001-2100	-	-	-	-
2101-2200	-	-	-	-
2201-2300	-	-	-	-
2301-2400	-	-	-	-
Totals	1,271	-	620	-

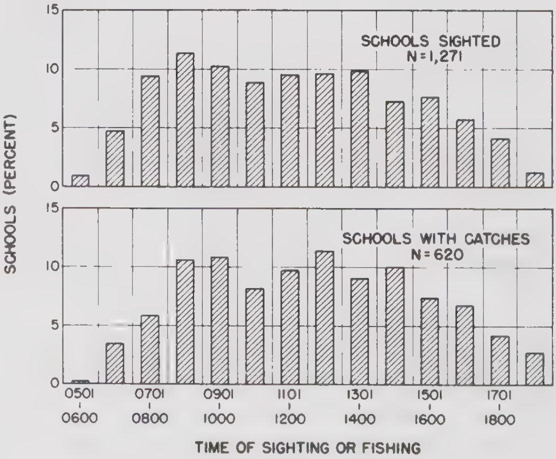

Figure 13.--Frequencies of school sightings and schools with catches, by time of day for seven Hawaiian skipjack tuna fishing vessels, June-August 1967.

is a general belief among the Hawaiian skipjack tuna fishermen that more bird flocks are sighted early in the morning and late in the afternoon. In contrast, another research cruise in June 1953 encountered a peak in sightings at 1100-1200 with a fairly large number of bird flocks sighted at all hours between 0700 and 1700. The lack of consistency among cruises also suggests that the dips and peaks in sightings result from changes in bird or fish behavior.

The spatial distribution of catches was similar to that of sightings (fig. 12). The percentage of schools with catches relative to sightings varied widely among the individual 20-minute areas of longitude and latitude, but the percentages calculated for larger sectors--east, west, north, and south of Oahu--varied little. It should be mentioned that the observers did not record the positions of some of the schools sighted, particularly those schools they encountered during their first week or two of sea duty. The reasons they gave were that they were seasick, were too far offshore, or were experiencing poor weather conditions which interfered with making a reasonably accurate estimate of the school's position. The recording of school positions improved as the observers became accustomed to sea life and learned to work closely with the captain and the fishermen.

In our calculations, we used only schools with positions recorded; therefore, the percentages are overestimates and are of value only in comparing one sector with another. Data presented in figure 5 showed that collectively, the percentage of schools with catches relative to sightings was only 47 percent, but by using only those schools with positions, we calculated that 60 percent of the schools sighted yielded catches. In sectors to the south and east of Oahu, the vessels caught fish from 62 and 61 percent, respectively, of the schools sighted, whereas in sectors to the west and north, they caught fish from 58 and 55 percent of the schools, respectively. Catch per school data from all four sectors ranged from 0.8 metric ton in the north to 1.2 metric tons per school in the west with intermediate values of 1.0 metric ton in the south and 1.1 metric tons in the east.

Table 14.--Number and percentage of trips tabulated by time meals were eaten aboard the seven Hawaiian skipjack tuna vessels, June-August 1967

Time	Breakfast		Lunch		Dinner	
	Number	Percent	Number	Percent	Number	Percent
0001-0100	-	-	-	-	-	-
0101-0200	-	-	-	-	-	-
0201-0300	-	-	-	-	-	-
0301-0400	-	-	-	-	-	-
0401-0500	9	6.9	-	-	-	-
0501-0600	103	79.2	-	-	-	-
0601-0700	18	13.9	-	-	-	-
0701-0800	-	-	-	-	-	-
0801-0900	-	-	-	-	-	-
0901-1000	-	-	15	8.7	-	-
1001-1100	-	-	83	48.0	-	-
1101-1200	-	-	42	24.3	-	-
1201-1300	-	-	21	12.1	-	-
1301-1400	-	-	9	5.2	-	-
1401-1500	-	-	3	1.7	-	-
1501-1600	-	-	-	-	1	0.9
1601-1700	-	-	-	-	8	7.6
1701-1800	-	-	-	-	33	31.1
1801-1900	-	-	-	-	46	43.4
1901-2000	-	-	-	-	16	15.1
2001-2100	-	-	-	-	2	1.9
2101-2200	-	-	-	-	-	-
2201-2300	-	-	-	-	-	-
2301-2400	-	-	-	-	-	-
Totals	130	-	173	-	106	-

The success of fishing in relation to the time of day followed a pattern similar to that seen for sightings relative to time of day (table 13 and fig. 13). Following a rapid increase in fishing success from daybreak to a peak at 0901-1000 and a dip at 1001-1100, there were two other peaks--one at 1201-1300 and another at 1401-1500.

There is also evidence that the vessels caught a large proportion of the day's catch, by weight, usually after 1200 (table 15). Dividing the day's total catch aboard each vessel by schools and by time of day, we found that usually the vessels had only 11 percent of the day's catch aboard by 0900, had less than half--37 percent--of the day's catch aboard by noon, then averaged 31 percent of the day's catch in both the third (1201-1500) and fourth (after 1501) quarters of the fishing day.

Cloud cover and wave height.--Fishing vessels usually operate under various weather conditions. Data collected at the time of fishing revealed that the vessels operated on days that were cloudless, cloudy, overcast, and rainy, and in seas varying from calm to very rough. We were, however, interested primarily in learning whether cloud cover or wave height had any effect on the biting behavior of skipjack tuna. Imamura (1949) reported that Japanese skipjack tuna fishermen experienced better fishing on cloudy days, but Yuen (1959) found that weather had no significant effect on biting behavior of skipjack tuna found in Hawaiian waters.

For June-August 1967, we found that for nearly 50 percent of the schools chummed, cloud cover at the time of fishing was three-tenths or less (table 16). Dividing the data into categories of schools with and without catches, we tested the probability of success in fishing relative to cloud cover and found that the ratios--success to failure--did not vary by more than chance ($\chi^2 = 10.60$; d.f. = 9; $p > 0.25$). We concluded that very cloudy, overcast, or rainy days probably affected fishing only by reducing the fishermen's chances of sighting schools.

Table 15.--Percentage of the day's total catch aboard the vessels in the first (by 0900), second (0901-1200), third (1201-1500), and fourth (after 1501) quarters of the fishing day for seven Hawaiian skipjack tuna fishing vessels, June-August 1967

Vessels	Quarters of the fishing day			
	First	Second	Third	Fourth
	Percent	Percent	Percent	Percent
A	3.3	31.5	42.4	22.8
B	15.5	15.3	35.4	33.8
C	17.0	20.2	23.7	39.1
D	9.2	24.9	35.2	30.7
E	7.1	41.6	28.5	22.8
F	7.2	40.9	33.3	18.6
G	16.4	10.3	21.0	52.3
All	10.8	26.4	31.4	31.4
Cumulative	10.8	37.2	68.6	100.0

Table 16.--Number and percentage of 619 schools with catches and 443 schools without catches, fished by seven Hawaiian skipjack tuna fishing vessels and tabulated by cloud cover at the time of fishing, June-August 1967

Cloud cover	Schools					
	With catches		Without catches		Total	
	Number	Percent	Number	Percent	Number	Percent
Cloudless	23	3.7	31	7.0	54	5.1
1/10 or less	128	20.7	91	20.5	219	20.6
2/10 and 3/10	146	23.6	89	20.1	235	22.1
4/10	83	13.4	67	15.1	150	14.1
5/10	63	10.2	49	11.1	112	10.5
6/10	60	9.7	28	6.3	88	8.3
7/10 and 8/10	42	6.8	35	7.9	77	7.3
9/10 and 9/10 plus	39	6.3	28	6.3	67	6.3
10/10	23	3.7	17	3.8	40	3.8
Rain	12	1.9	8	1.8	20	1.9

The height of the waves also had little effect on fishing. Our data showed that most fishing occurred in waters with moderate wave height; only nine schools were chummed in waters considered very rough (table 17). Testing the ratios of the number of schools with catches to those without, relative to the height of the waves at the time of fishing, we found that they were reasonably constant, with the exception of those schools chummed in very rough waters ($\chi^2 = 0.42$; d.f. = 2; $p > 0.75$).

Predominant birds and size of bird flocks.--While pursuing a school, skipjack tuna fishermen rely heavily on the behavior, species, and number of birds in the flocks to give them information about the species, size, and movement of the fish. For example, Japanese tuna fishermen know from the birds' wild horizontal flights that a school is near the surface, and from the birds' slow flight, high above the water, that the school is swimming deep (Imamura, 1949).

In examining the relationships of catches with predominant birds and with bird flock size at the time of fishing, we found that petrels and shearwaters were most frequently associated with skipjack tuna schools. Of 1,235 flocks identified to predominant species, petrels and shearwaters predominated in 963 flocks or 78 percent, whereas terns predominated in only 235 flocks or 19 percent. Small flocks of boobies or frigate birds predominated infrequently. Using only data for schools chummed (table 18), we found that the predominant species associated with the school at the time of fishing was not a good indicator of success in fishing ($\chi^2 = 2.25$; d.f. = 3; $p > 0.50$).

Rather than predominant species, the size of the bird flock associated with the school appeared to be a good indicator of fishing success. Bird flocks accompanying fish schools varied in size from fewer than 10 to several hundred birds, so to simplify estimation we used only three categories: 10 or fewer, 11 to 50, and 50 or more birds. Size estimates of 1,249

Table 17.--Number and percentage of 620 schools with catches and 442 schools without catches, fished by seven Hawaiian skipjack tuna fishing vessels and tabulated by the height of the wave at the time of fishing, June-August 1967

Wave height	Schools					
	With catches		Without catches		Total	
	Number	Percent	Number	Percent	Number	Percent
Calm (<0.3 m.)	34	5.5	32	7.2	66	6.2
Moderate (0.3-1.5 m.)	471	75.9	331	74.9	802	75.5
Rough (1.5-3.7 m.)	107	17.3	78	17.7	185	17.4
Very rough (>3.7 m.)	8	1.3	1	0.2	9	0.9

Table 18.--Number and percentage of 613 schools with catches and 437 schools without catches, fished by seven Hawaiian skipjack tuna fishing vessels and tabulated by types of predominant birds in the flock associated with the schools at the time of fishing, June-August 1967

Predominant birds	Schools					
	With catches		Without catches		Total	
	Number	Percent	Number	Percent	Number	Percent
Tern	120	19.6	78	17.8	198	18.8
Petrel-shearwater	470	76.7	349	79.9	819	78.0
Booby	17	2.8	7	1.6	24	2.3
Bo'sun bird	2	0.3	3	0.7	5	0.5
Frigate bird	1	0.2	-	-	1	0.1
Other birds	3	0.4	-	-	3	0.3

flocks showed 700 (56 percent) consisted of 50 or more birds, 458 (37 percent) had 11-50 birds, and 91 (7 percent) had 10 or fewer birds. Tabulating only those schools chummed, by size of the flock, we tested the ratios of the number of schools with catches to those without and found them differing significantly ($\chi^2 = 66.60$; d.f. = 2; $p < 0.01$). Table 19 shows that of 617 schools with catches, most had 50 or more birds (68 percent), whereas of 437 schools without catches, most had only 11-50 birds (47 percent). Actually, of 607 schools associated with 50 or more birds, 7 out of 10 schools yielded catches.

Catch Per Trip

The amount of fish caught per school influences the catch per trip, which has been tabulated by weight of fish in table 20. The distribution of catch per trip was skewed and in 244 trips, of which 22 or 9 percent ended in zero catches, most had 0.1-1.0 metric ton. Actually, slightly more than half (55 percent) of the catches were 3.0 metric tons or less per trip. Vessel F, the low producer among the vessels, averaged 2.0 metric tons per trip, whereas vessel A, the high producer, averaged twice as much or 4.1 metric tons (table 3). The grand mean was 2.8 metric tons or about 376 fish per trip.

Strongly skewed toward small catches, the distribution of catch per school in table 21 shows that the vessel usually caught between 0.1 and 0.5 metric ton or between 1 and 100 fish. Actually, catches ranged from 1 kg. to 9.0 metric tons or from 1 to 1,710 fish, and averaged 1.1 metric tons or 148 fish, slightly higher than the positions of the modes in the

Table 19.--Number and percentage of 617 schools with catches and 437 schools without catches, fished by seven Hawaiian skipjack tuna fishing vessels and tabulated by size of bird flocks associated with the schools at the time of fishing, June-August 1967

Size of bird flock	Schools					
	With catches		Without catches		Total	
Number	Number	Percent	Number	Percent	Number	Percent
10 or fewer	26	4.2	42	9.6	68	6.4
11 to 50	172	27.9	207	47.4	379	36.0
50 or more	419	67.9	188	43.0	607	57.6

Table 20.--Number of trips, schools, catch per trip, catch per school, and number of schools fished per trip, tabulated by the weight of fish caught per trip by seven Hawaiian skipjack tuna vessels, June-August 1967

Size of catch	Trips	Schools	Catch per trip	Catch per school		Schools per trip
Metric ton	Number	Number	Number	Number	Metric ton	Number
0	22	-	-	-	-	-
0.1-1.0	53	103	130.6	67.2	0.3	1.9
1.1-2.0	41	113	256.3	93.0	0.6	2.8
2.1-3.0	41	131	503.8	157.7	0.8	3.2
3.1-4.0	26	71	512.2	187.6	1.3	2.7
4.1-5.0	23	73	514.9	162.2	1.4	3.2
5.1-6.0	12	36	847.2	282.4	1.9	3.0
6.1-7.0	12	45	638.3	170.2	1.8	3.8
7.1-8.0	6	18	659.0	219.7	2.5	3.0
8.1-9.0	4	18	830.3	184.5	1.9	4.5
9.1-10.0	1	6	865.0	144.2	1.6	6.0
10.1-11.0	2	6	1,002.5	334.2	3.6	3.0
11.1-12.0	-	-	-	-	-	-
12.1-13.0	1	3	1,015.0	338.3	4.1	3.0

distributions because of the long positive tails. Catch per school ranged among the vessels from 0.7 metric ton per school for vessel F to 1.4 metric tons per school for vessels B and C (table 3).

Another component which influenced catch per trip was the number of schools with catches on a trip. Table 3 shows that vessels A and G were most successful, catching fish from an average of 3.1 schools per trip, that vessel B was least successful, catching from an average of only 1.8 schools, and that on 231 trips, the vessels usually caught fish from 2.5 schools per trip. The distribution of trips, tabulated by the number of schools with and without catches, was skewed toward fewer schools per trip, with the mode at two schools and the range from one to eight schools with catches per trip (table 4 and fig. 5).

The relationship of catch per trip with catch per school and number of schools fished is shown in table 20 and figure 14. We found that usually 1.9 schools yielded catches averaging 0.3 metric ton per school on trips with catches of 0.1 to 1.0 metric ton. The average number of schools fished and the average catch per school tended to increase progressively for larger categories of catch per trip and reached 3.0 schools and 2.5 metric tons per school, respectively, for those trips with catches of 7.1 to 8.0 metric tons. At 8.1 to 9.0 metric tons per trip, the average number of schools increased further to 4.5 schools, but the average catch per school declined to 1.9 metric tons. There were few trips with catches of 9.1 metric tons or more; therefore, although we calculated averages for the number of schools fished and school catches, they were not considered representative and were excluded from the discussion.

SUPPORTING ACTIVITIES

In addition to time spent traveling, baiting, scouting, and fishing, the fishermen also are engaged in unloading the catch, loading ice, and fabricating, repairing, and maintaining their gear and vessels. We collected and analyzed data on two of these operations--unloading the catch and loading ice.

Upon return to Kewalo Basin with the day's catch, the crew unloads by hand if the catch is small or if part of the catch is consigned to the fresh-fish market. After the market fish is unloaded, the crew uses a conveyor to unload the balance into trucks for sale to the cannery. At Kaneohe Bay, however, the crew unloads the entire catch by hand. In calculating the unloading time for each vessel, we made no distinction in the method used in unloading the catch. The vessels usually loaded ice after the baitwells were emptied of fish.

Table 21.--Size of catch, number of schools, and catch per school of seven Hawaiian skipjack tuna vessels, June-August 1967

Size of catch	Schools	Catch per school	Size of catch	Schools	Catch per school
Number	Number	Metric ton	Metric ton	Number	Number
0	449	-	0	449	-
1-100	326	0.4	0.1-0.5	283	54.3
101-200	146	1.2	0.6-1.0	133	145.6
201-300	71	2.1	1.1-1.5	75	204.9
301-400	35	2.5	1.6-2.0	34	224.8
401-500	20	2.8	2.1-2.5	32	243.1
501-600	7	4.6	2.6-3.0	17	401.8
601-700	7	2.3	3.1-3.5	14	393.5
701-800	4	3.5	3.6-4.0	14	322.6
801-900	1	1.5	4.1-4.5	5	342.4
901-1,000	1	1.7	4.6-5.0	6	456.8
1,001-1,100	2	2.1	5.1-5.5	2	451.5
1,101-1,200	-	-	5.6-6.0	3	506.0
1,201-1,300	-	-	6.1-6.5	2	530.5
1,301-1,400	-	-	6.6-7.0	1	535.0
1,401-1,500	-	-	7.1-7.5	-	-
1,501-1,600	1	2.9	7.6-8.0	1	651.0
1,601-1,700	1	3.3	8.1-8.5	-	-
1,701-1,800	1	2.7	8.6-9.0	1	740.0

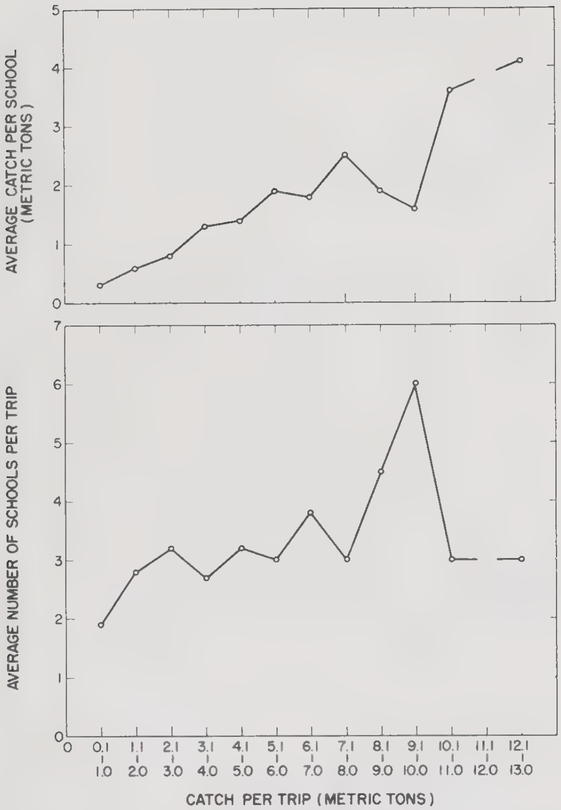

Figure 14.--Relation between catch per trip and average number of schools fished and average catch per school by seven Hawaiian skipjack tuna fishing vessels, June-August 1967.

From data on unloading catch and loading ice, we found that the weight of fish unloaded varied among the vessels from an average of 2.4 to 4.1 metric tons and collectively averaged 3.4 metric tons. In table 3, we noted that catch per trip was 2.8 metric tons, a figure somewhat lower than the average of 3.4 metric tons unloaded at the docks. The discrepancy between the catch per trip and the average catch unloaded occurs because catch per trip was based on a single day's fishing, whereas the unloaded catch included, in some cases, the catches of 2 or more days of fishing.

Usually about 9 men, including crewmembers and shoreside helpers, unloaded the vessel, with a range of 7 to 13 men. Unloading usually required about one-half hour; the average unloading time among the vessels ranged from 26.8 to 33.0 minutes.

The rate of unloading depended largely on the size of the fish. Vessels which caught small fish usually had low unloading rates. On the contrary, vessel B, which had the highest unloading rate per man-minute at 16.8 kg., caught fish which averaged 9.5 kg., the largest average among the vessels.

In loading ice, the vessels averaged from 3.7 to 11.4 minutes with a grand mean of 6.6 minutes. Since loading ice is at a fixed rate, the loading time varied directly with the quantity loaded.

OPTIMUM VESSEL OPERATION

There appears to be a certain pattern to a successful operation in the fishery for skipjack tuna in Hawaiian waters. Using catch, which is convertible into earnings as a measure of success, we found that certain characteristics differ between a high- and low-producing vessel.

There were several aspects of the operations of vessel F, a low producer, which contrasted sharply with those of vessel A, a high producer. Both were below average in pursuit time, but vessel A pursued its schools almost twice as long as vessel F. Vessel A chummed its schools slightly longer than average; vessel F only about half as long as the average of all vessels. In fishing, vessel A, which averaged slightly longer than vessel F in fishing per trip and per school, had values higher than the seven-vessel averages in these categories. In number of men hooking per school, vessel F had six men, which is not dissimilar from the seven-vessel average, but vessel A usually had seven men fishing.

Moreover, vessel A used unusually large amounts of bait at sea, averaging about 23 buckets per trip, whereas vessel F used only about 9 buckets, which is 25 percent less than the average for the seven vessels. A similar difference between these vessels can be seen in the average amount of bait used per school. Vessel A succeeded in fishing 64 percent of the schools it sighted, whereas vessel F succeeded in fishing only 56 percent of its schools.

More time spent pursuing and chumming the schools, more men available for fishing, and more bait used per school undoubtedly contributed to a larger catch per school for vessel A. Averaging 1.3 metric tons per school, vessel A usually caught nearly twice as much per school as vessel F, which averaged only 0.7 metric ton.

Data on catch per bucket of bait used in fishing, however, cast doubt that the operation of vessel A was most successful among the vessels. Vessel A, which ranked among the lowest, caught only 179.3 kg. of skipjack per bucket of bait compared with vessel F, which ranked above average with catches of 225.3 kg. per bucket (table 3).

A vessel with a high catch rate per bucket of bait used may be termed efficient in its bait use, but if the bait conserved dies before it can be used in fishing, then it appears that a vessel with a lower catch rate per bucket of bait is just as efficient if a high percentage of its bait results in production of fish. From examination of the Aku Catch Reports at the Hawaii State Division of Fish and Game, we found that vessel A used 78 percent of the bait it caught, whereas vessel F used only 59 percent. The fact that vessel A had the largest bait capacity among the seven vessels and vessel F the smallest also accounts for the rates at which both vessels used their bait in fishing. Evidently vessel F was too economical with bait and the result was that it had smaller catches and fewer successes in fishing the schools. Overall, the seven vessels used about 66 percent of the bait they caught.

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BIOMASS OF THE SUBPOPULATIONS OF NORTHERN ANCHOVY *ENGRAULIS MORDAX* GIRARD

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During the California Cooperative Oceanic Fisheries Investigations (CalCOFI) anchovy larvae have been collected by standard methods described by Ahlstrom (1948, 1953) on a standard station plan (inside back cover) in waters off the west coast from Oregon to the tip of Baja California every year 1951–1966 and in 1969. The data from 1951 through 1958 is shown by year, month, station and size group of larvae in 269 charts of the area in CalCOFI Atlas No. 9, 1968, which also includes a brief account of methods, with references. The total number of larvae each year in the known range of the northern anchovy *Engraulis mordax,* calculated by methods discussed in Ahlstrom (1968) and Messersmith, Baxter and Roedel (1969) is shown in the last column of Table 1.

The biomass of spawning anchovy adults was calculated from $B_a = 98.2\ L_a$ where B_a is the biomass in millions of tons and L_a is the number of larvae times 10^{12} (Smith, MS). The standard error of prediction is about 9%. The biomass each year for the entire region survey area is shown in Figure 1 and given in the last column of Table 2. The biomass increased from about 640,000 tons in 1951 to over 6 million tons in 1962. Since 1962 it has remained high, fluctuating between about 5 and 8 million tons. The preliminary estimate for 1969 based on those collections which have been sorted and counted to date is 5.4 million tons.

These figures represent all the northern anchovies which spawn off the coast from San Francisco to Cape San Lazaro, Baja California, Mexico. McHugh (1951), from a study of variations in certain meristic characters of *E. mordax,* concluded that three geographic-

TABLE 1

Numbers × 10^{12} of anchovy larvae (regional census estimates, Smith, MS) in four geographical areas.

Year	Northern subpopulation	Central subpopulation		Southern subpopulation	Total
	Central California	Southern California	Northern Baja Calif.	Southern Baja Calif.	
1951	111	1,474	1,525	3,394	6,504
1952	76	879	3,301	3,876	8,132
1953	2	4,446	3,774	5,410	13,632
1954	1,164	6,041	2,671	8,657	18,533
1955	24	4,864	9,249	2,963	17,100
1956	247	3,294	6,071	5,603	15,215
1957	130	11,799	4,257	3,854	20,040
1958	3,930	11,655	7,003	5,684	28,272
1959	3,506	12,439	4,729	2,789	23,463
1960	637	8,791	10,748	11,238	31,414
1961	1,054	7,518	5,357	18,609	32,538
1962	979	23,102	21,324	18,353	63,758
1963	1,577	32,745	16,763	10,448	61,533
1964	5,221	34,046	5,330	7,656	52,253
1965	1,256	49,634	13,631	14,771	79,292
1966	4,001	35,360	6,947	5,892	52,200

TABLE 2

Spawning biomass in thousands of tons of anchovies in each of the three subpopulations (Smith, MS).

Year	Northern subpopulation	Central subpopulation	Southern subpopulation	Total
1951	11	294	333	639
1952	7	410	381	798
1953	0	807	531	1,388
1954	114	855	850	1,820
1955	2	1,386	291	1,679
1956	24	919	550	1,494
1957	13	1,576	378	1,967
1958	386	1,832	558	2,776
1959	344	1,686	274	2,304
1960	63	1,918	1,103	3,084
1961	103	1,264	1,827	3,194
1962	96	4,362	1,802	6,260
1963	155	4,861	1,026	6,041
1964	513	3,866	752	5,130
1965	123	6,211	1,450	7,785
1966	393	4,154	578	5,125

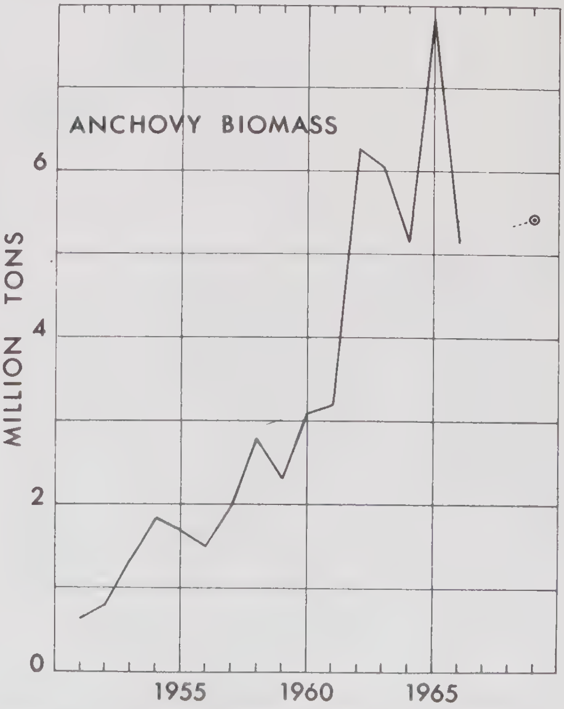

FIGURE 1. Total spawning biomass of anchovies in the CalCOFI survey area, calculated from the numbers of anchovy larvae collected each year.

ally separate subpopulations could be found over this range and suggested as approximate boundary markers Point Conception on the California coast and Cedros Island off Baja California. Genetic studies on adult anchovies, using serum transferrins (Vrooman and Paloma, MS), confirm McHugh's findings of three subpopulations and also show that the winter distribution of the three groups generally fits his description. Figure 2 is a schematic representation of the distribution of the subpopulations.

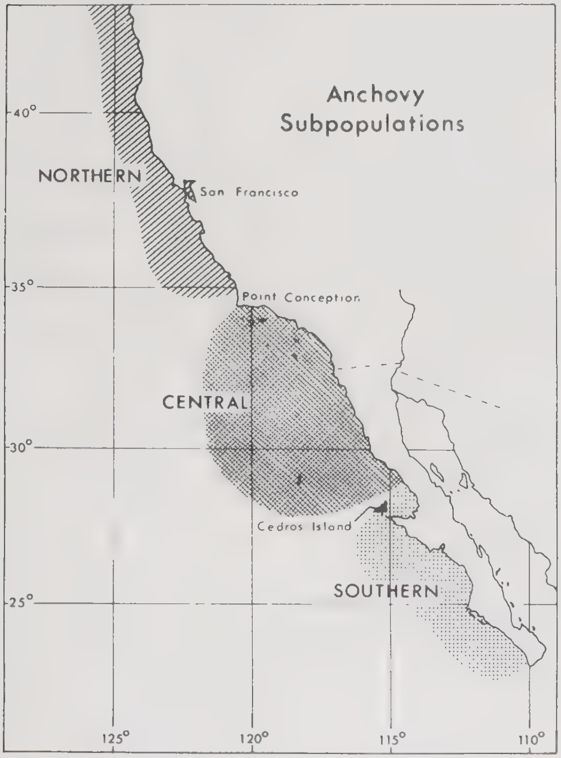

FIGURE 2. Schematic diagram of the winter distribution of the three subpopulations of the northern anchovy, *Engraulis mordax*.

When the CalCOFI grid is divided into four areas and the numbers of anchovy larvae in each is used as an index of abundance, geographical differences in changes of biomass with time may be seen. The four areas are 1) Central California—all CalCOFI station lines between San Francisco and Point Conception, 2) Southern California—Point Conception to Ensenada, Baja California, 3) Northern Baja California—Ensenada to Cedros Island, and 4) Southern Baja California—Cedros Island to Cape San Lazaro. From this data (Table 1, Figure 3) it can be seen that the greatest increase by far has taken place in the Southern California area.

By combining the Southern California and Northern Baja California areas the larvae are divided roughly into the three subpopulations (Figure 4). Table 2 shows the biomass of spawning adults as calculated from this data. From these representations it is apparent that although during 1960–66 the biomass of the southern subpopulation was on the average twice as great as during 1951–59, the ratio for the same periods in the central subpopulation was three and a half. The ratio for the northern subpopulation was intermediate.

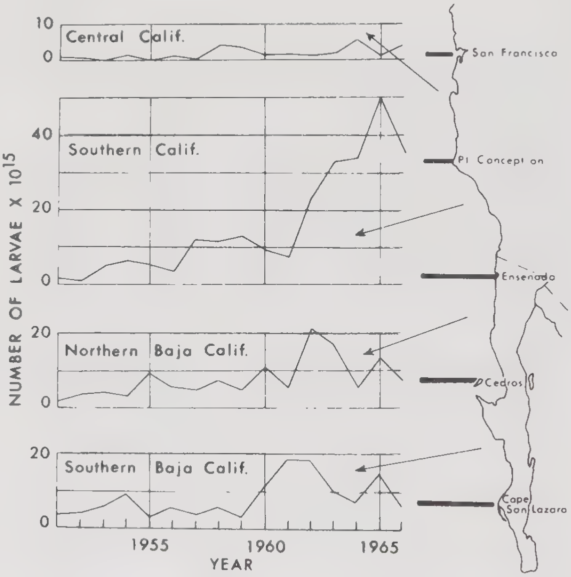

FIGURE 3. Regional census estimates of northern anchovy, *Engraulis mordax*, for the years 1951–1966 (Smith, MS).

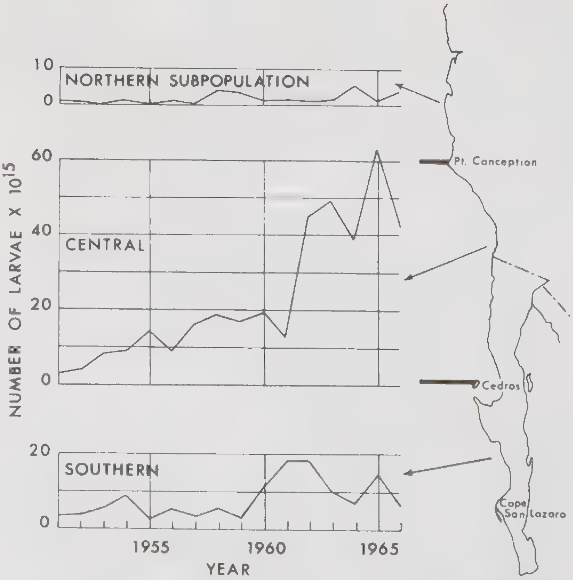

FIGURE 4. Regional census estimates of northern anchovy larvae for each of the three subpopulations in the CalCOFI area, 1951–1966.

The number of larvae may be used as a fair approximation of the total biomass of adult anchovies in the central subpopulation because the cruise pattern covered essentially their whole range at all seasons in all years. In the northern region collections of larvae have been made as far north as the California-Oregon border, but not with sufficient regularity and geographic coverage to make a satisfactory basis for calculating the total biomass of the northern subpopulation. The situation is the same for the southern subpopulation south of Cape San Lazaro. Details of the area covered and the stations occupied are given by Ahlstrom (1966).

Vrooman and Paloma (lc) observed a considerable shift of the central subpopulation north in the summer and south in the winter. These authors noted that in winter and early spring when most of the anchovy spawning takes place, the boundary between the northern and central subpopulations is as shown in Figure 3. Also, Haugen, Messersmith and Wickwire (1969) observed that a few of the anchovies tagged in the central California region were recovered in southern California and vice versa. These findings we believe do not impair the evidence of an essential distinction between the northern and central subpopulations.

Within the CalCOFI area between San Francisco and Cape San Lazaro, the mean total biomass of anchovies for the five year period 1962–66 was 6.1 million tons. The central subpopulation amounted to 4.7 million tons or 77.3% of that total. The southern subpopulation, with about 1.1 million tons, made up 18.5%, while the northern subpopulation contributed only 0.26 million tons or 4.2% of the 5-year mean.

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BIOLOGY OF THE PILE PERCH, Rhacochilus vacca, IN YAQUINA BAY, OREGON

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ABSTRACT.--Growth, reproduction, food habits, and parasites of pile perch, Rhacochilus vacca (Girard), were investigated in Yaquina Bay, Oreg., between April 1966 and July 1967. The research disclosed that pile perch live at least 10 years. Males and females of given ages are close to the same size up to age IV, after which females are increasingly larger than males. Males and females respectively approach average ultimate sizes of 1,120 g at 430 mm and 2,000 g at 490 mm total length. Some females mature in their second year; 90 percent mature at age III. Some males also mature in their second year. Mating occurs in the fall; there is a delay of about 3 months before fertilization. The gestation period is about 6½ months; most young are born between late June and early August. Fecundity increases with size and age of fish (observed range 7 to 61 embryos). Dead eggs and malformed embryos are occasionally found among healthy embryos, the occurrence of malformed embryos being inversely related to age of parent, the occurrence of dead eggs being independent of age of parent. Pile perch are carnivorous feeders, obtaining food from the bottom or protruding surfaces in the littoral zone. The diet varies between seasons and localities. Principal foods are barnacles, mussels, the bay clams, crabs, mud shrimp, and a tube dwelling amphipod. None of the pile perch examined was heavily parasitized. Infestations of gill copepods vary seasonally.

The pile perch (Rhacochilus vacca), a member of the surfperch family (Embiotocidae), ranges from southeastern Alaska to northern Baja California (Tarp, 1952). It can be recognized by its high anterior dorsal fin rays which form a prominent peak in the contour of the fin and by its silvery color variably overlain with sooty tones which usually include a single dark verticle bar slightly posterior to the middle of the body. Its preference for near-shore areas, bays, and docks makes it easily accessible to fishermen. This coupled with its size and palatability, makes it a valuable recreational resource. An angler survey by Parrish (1966) showed that the pile perch was the third most important fish by weight caught by sport fishermen in Yaquina Bay, Oreg. Morgan (1961) reported it as the most abundant embiotocid in Siletz Bay, Oreg. and Tarp (1952) listed it as a moderately important commercial species.

Most published information on the biology of the pile perch concerns reproduction and population movements. Wales (1929) observed a large school of pile perch mating in water

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about 15 feet deep at the fish wharf in Monterey, Calif., on December 20, 1928. Rechnitzer and Limbaugh (1952) noted that pile perch began giving birth about the middle of April in the ocean near La Jolla, Calif. Morgan (1961) found that the pile perch population in Siletz Bay, Oreg. is migratory and that the population size is at its peak in the upper part of the Bay from June to July, when it consists mostly of gravid females. He also found that most females had produced young by late August.

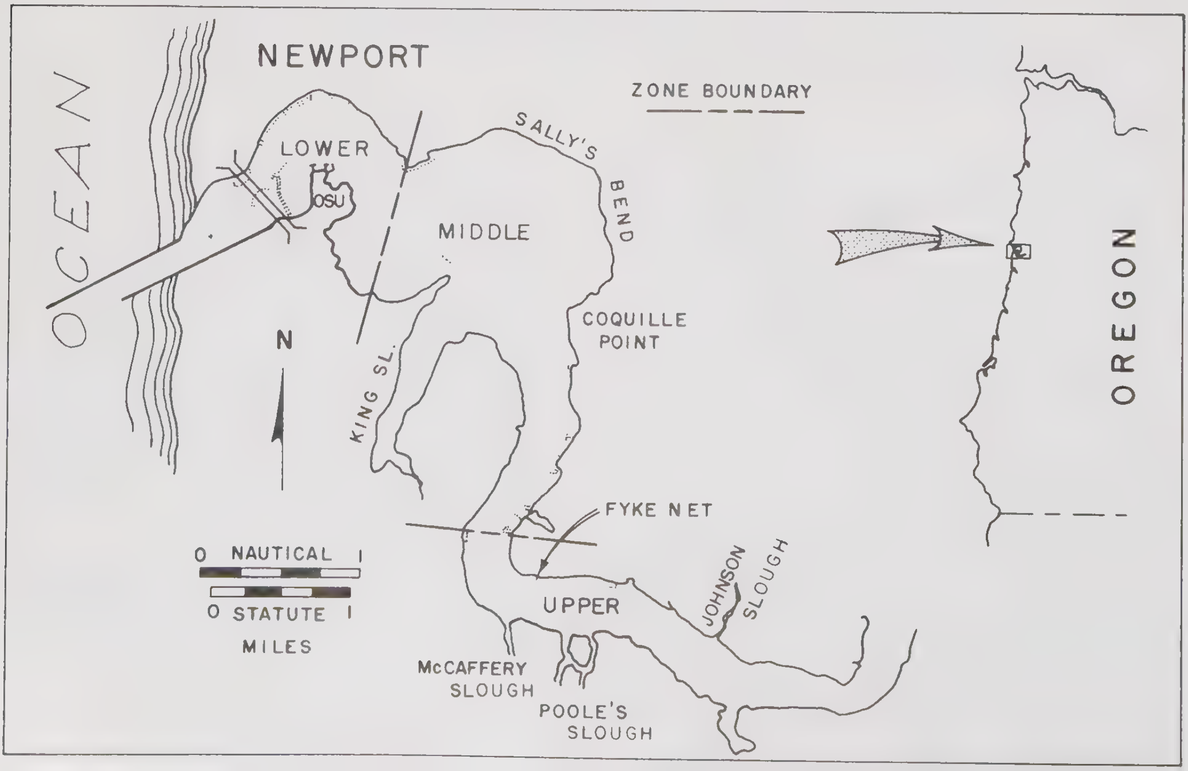
The present study was conducted in Yaquina Bay, estuary of the Yaquina River, which communicates with the Pacific Ocean between mile-long jetties at the town of Newport on the central Oregon coast. The estuary is divided into a lower, a middle, and an upper zone, each with a distinct aquatic environment (fig. 1). The lower zone is characterized by strong tidal currents, scoured sandy bottom, and nearly constant ocean salinity. The middle zone is characterized by extensive mud flats with eel grass (*Zostera*) beds, moderate currents, soft silty bottom, and moderately fluctuating salinity. The upper zone is characterized by firm mud-gravel bottom, fairly strong currents, and highly fluctuating salinity (both tidally and seasonally). These zones coincide with the three realms of sediment deposition defined by Kulm and Byrne (1966): marine, marine-fluviatile, and fluviatile. Precipitation in the area is seasonal, with 80 to 90 percent of the annual average of 65 inches falling between September and May, primarily in the form of rain (Kulm and Byrne, 1966).

I am grateful to Dr. Howard E. Horton, who acted as major professor, for suggesting the study and for his advice throughout the study. Thanks are also due Dr. Alan J. Beardsley for assistance in collecting specimens and the Fish Commission of Oregon for generously providing a large steel fyke net for the study.

AGE AND GROWTH

Method of age determination

Length-frequency data from this study were of no value in distinguishing age classes of



pile perch above age I, partly because of the lack of a large sample obtained over a short time. The scale method of age determination, used successfully in aging other embiotocids (Carlisle, Schott, and Abramson, 1960; Sivalingam, 1956; Hubbs, 1921), was employed. An attempt was made to collect fish throughout the year, but success was poor in winter. Gill nets, a seine, an otter trawl, a fyke net, and hook and line gear were all used at various times during the study, making it possible to collect specimens of all age classes in the population. All lengths and weights were obtained in the field from freshly killed specimens, except for young-of-the-year fish which were first preserved in 10 percent formalin.

To achieve uniformity, a specific scale located five rows below the lateral line in the scale column originating below the third dorsal spine was taken from each side of the body. When one of these "key scales" was found to be regenerated, an adjacent (anterior or posterior) scale was used. Scale features were studied and measurements were made from acetate impressions projected with an Eberbach projector. Typical scales of pile perch and the method of measuring annuli and scale radius are shown in figure 2. The metamorphic "annulus" is a recognizable check formed approximately at the time of birth.

Because fish were collected during all months of the year, a "birthday" was needed for assigning ages, and January 1 was chosen. Thus, because annuli were formed from March through June, fish caught in January and February were assigned ages greater by 1 than their number of annuli. Assignment of ages for fish caught from March through June required in each case judgement whether the current year's annulus had been formed. These judgements were made on the basis of scale growth beyond the last annulus. Total lengths (TL) at previous ages were calculated by the direct-proportion formula with correction factor (Rounsefell and Everhart, 1953). The calculations were performed by computer.

Growth rates

Regression analysis of key scale radius on total length for 218 pile perch yielded the equation $Y = 0.67X - 20.75$ with a correlation coefficient (r) of 0.9835. The apparent total length of pile perch at the time of scale formation (x-intercept) was 31 mm. This was used as the correction factor in the back-calculation formula.

Males and females grew at about the same rate for the first 3 or 4 years, after which the growth rate of males declined more rapidly than that of females (fig. 3). The apparent increase in growth rates for females during the eighth and ninth years is probably not real. Two factors tend to diminish the reliability of average back-calculated lengths as age increases: increasing proportion of erroneous age determinations and decreasing size of sample. Back-calculations were based on the following numbers of males and females, respectively, in each age-class: I, 4 and 2; II, 9 and 2; III, 6 and 14; IV, 11 and 41; V, 11 and 71; VI, 11 and 33; VII, 19 and 28; VIII, 7 and 15; IX, 9 and 4; X, 0 and 3.

Total lengths (in millimeters) may be converted to standard lengths (SL) (in millimeters) by the formula $SL = 0.75TL - 1.51$. This equation was derived graphically from data on 12 male and 8 female pile perch ranging in size from 76 mm to 398 mm TL.

Growth transformations (Walford, 1946) indicated maximum attainable total lengths (TL_∞) of 432 mm for male and 490 mm for female pile perch (fig. 4).

Rosa Lee's phenomenon as presented by Ricker (1958) appeared to be absent. Growth rates of young fish did not appear to be slower (or faster) when calculated from scales of older fish than when calculated from scales of younger fish. This is as would be expected, since the sport fishery for pile perch is not selective for the faster (or slower) growing individuals.

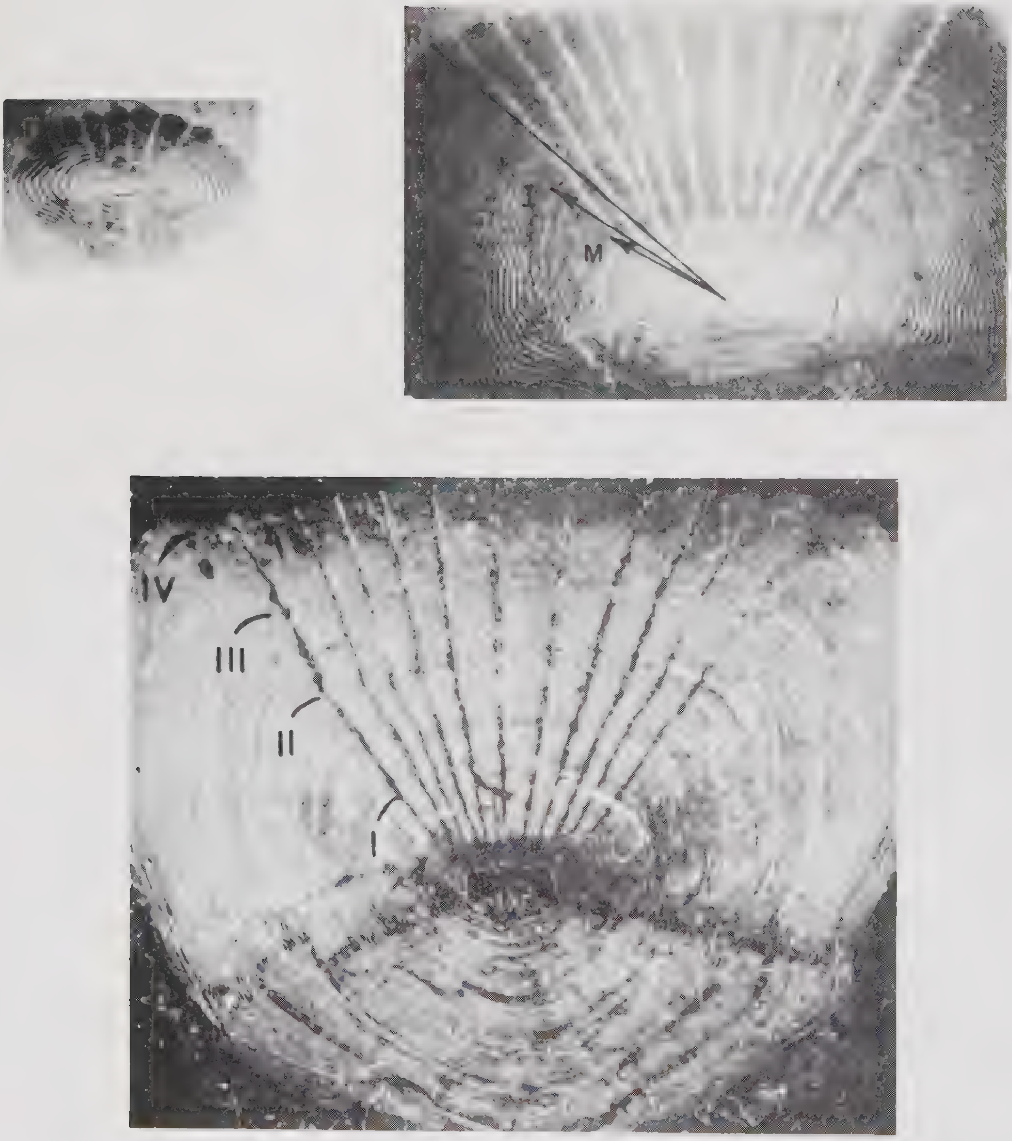


Figure 2.--Scales of pile perch. a, Near-term embryo 59 mm standard length. b, Age II perch captured just before annulus formation showing measurement of metamorphic "annulus" M, annulus I, and total scale radius R. c, Age IV female showing regenerated focus. (a and b are of the same magnification, c is less magnified.)

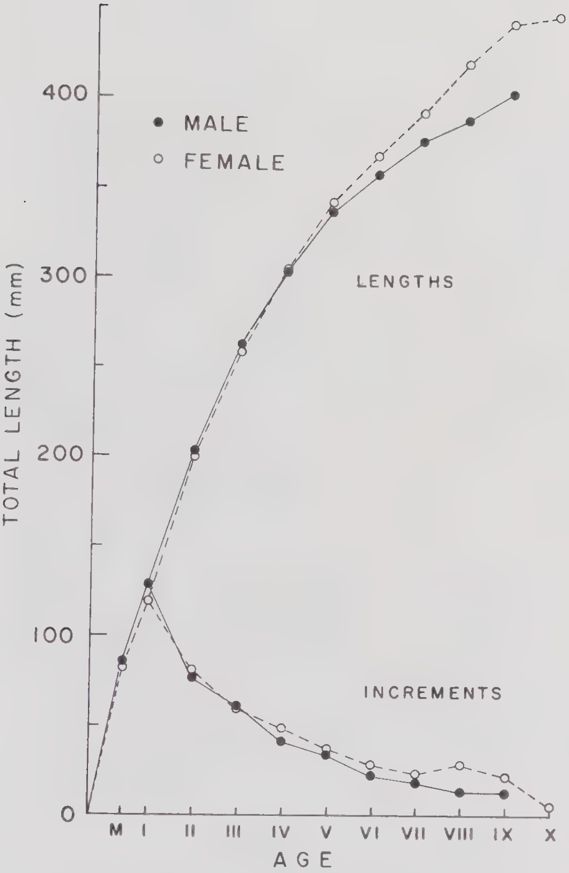


Figure 3.--Mean back-calculated lengths at each annulus and annual increments in length for 87 male and 231 female pile perch. Age M refers to length at formation of the metamorphic annulus, or the approximate length at birth.

Weight-length relations

In figure 5 the relation of weight to length is illustrated on a linear scale for each sex. For females, only those without embryos or those with embryos less than 33 mm SL were included in analysis of the weight-length relation. The general exponential relation of weight to length $W = cL^n$ was assumed. Regression lines fitted by least squares to the logarithms of lengths and weights had the following equations:

$\mathrm{Log}_{10}W = 3.08\ \mathrm{Log}_{10}L - 5.06$ (males) and

$\mathrm{Log}_{10}W = 3.19\ \mathrm{Log}_{10}L - 5.29$ (females)

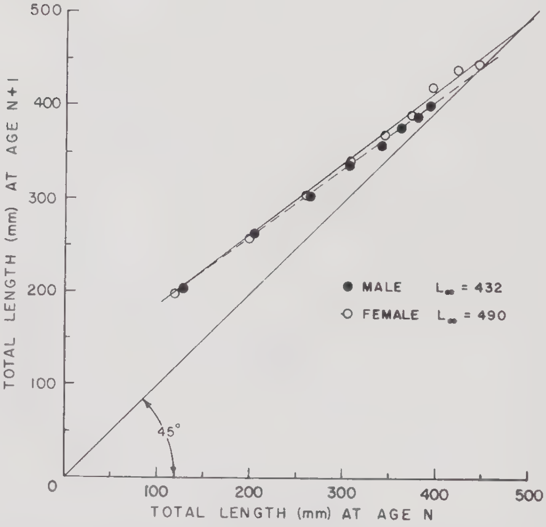


Figure 4.--Eye-fitted growth transformations based on mean back-calculated lengths of 87 male and 231 female pile perch.

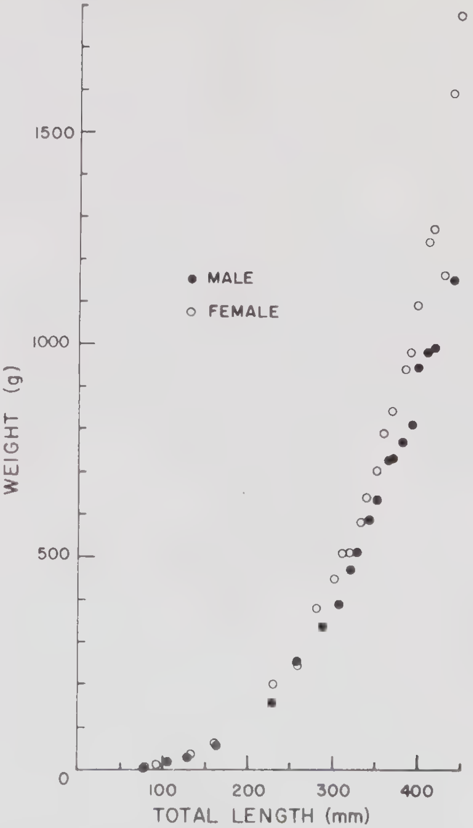


Figure 5.--Mean weights compared to mean lengths at various length intervals for male and female pile perch. Females with embryos larger than 30 mm SL

where W = body weight in grams and L = total length in millimeters. Correlation coefficients (r) of data in these equations are 0.9996 and 0.9993 respectively. Growth in weight and annual increments in weight are shown in figure 6. Average weights at each annulus were calculated by inserting mean back-calculated lengths in the regression equations for weight on length.

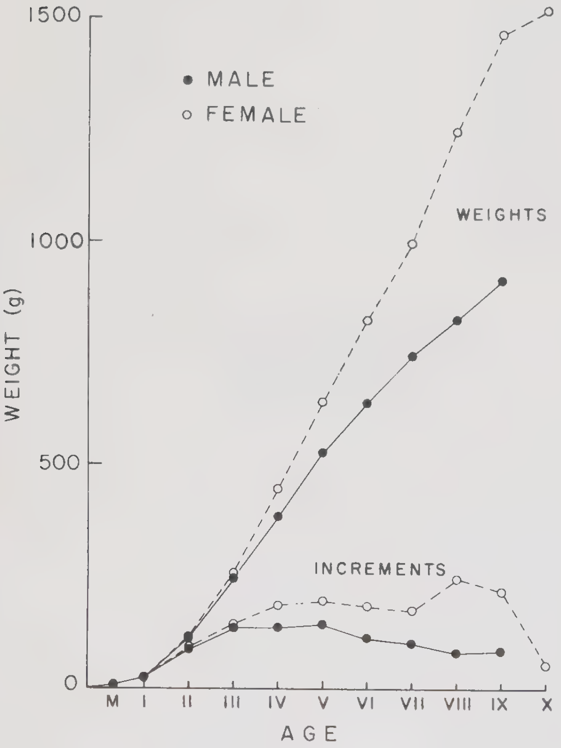


Figure 6.--Calculated mean weights at each annulus and annual increments in weight for male and female pile perch.

Distribution within the bay by sex and age

Pile perch appeared to enter the estuary in spring and to leave it in the fall, as catch per effort was very low in late fall and winter and high in spring and summer. Morgan (1961) found a similar migratory pattern for pile perch in Siletz Bay, Oreg. During the spring and summer the sexes were partially segregated in Yaquina Bay, the catches dominated by males in the lower zone, by females in the upper zone, and mixed in the middle zone.

It became apparent during the study that age classes I, II, and III were captured less frequently than expected, though young-of-the-year pile perch and other small fish were captured with the seine, otter trawl, and experimental gill nets. A catch curve (fig. 7) for pile perch caught with these types of gear confirms the low abundance for these early age classes. Apparently these young fish tend to remain out of the estuary after leaving during their first winter; it seems unlikely that these age classes were present in the Bay but concentrated in areas separate from the older fish, as many areas were sampled and nowhere were more than one or two individuals of these ages captured at one time.

REPRODUCTION

In embiotocids the male gonads are separate, except for the ducts which unite and exit through the urinogenital opening. In females the gonads are fused into a single bilobed organ which is internally divided lengthwise by several membranes called ovarian septa. The eggs are produced on the septa and expelled from the follicles into the chambers between the septa either just before or just after fertilization. The septa also provide surface area for gas exchange between maternal and embryonic blood supplies. The vertical fins of the embryos are well vascularized and greatly enlarged for this purpose. The embryos remain free within the ovary until birth and receive nourishment by ingesting ovarian secretions. The yolk is small and provides nourishment for only a small fraction of intraovarian development (Triplett, 1960; Engen, 1968). The term "embryo" is used in this paper in reference to the young in all stages prior to birth.

Methods of study

Data on reproduction were gathered by examination of reproductive tracts of pile perch obtained throughout the study. Maturity of male reproductive organs was assessed by an index calculated as follows:

$$\frac{\text{testis length (mm)} \times \text{testis width (mm)}}{\text{fish weight (g)}}$$

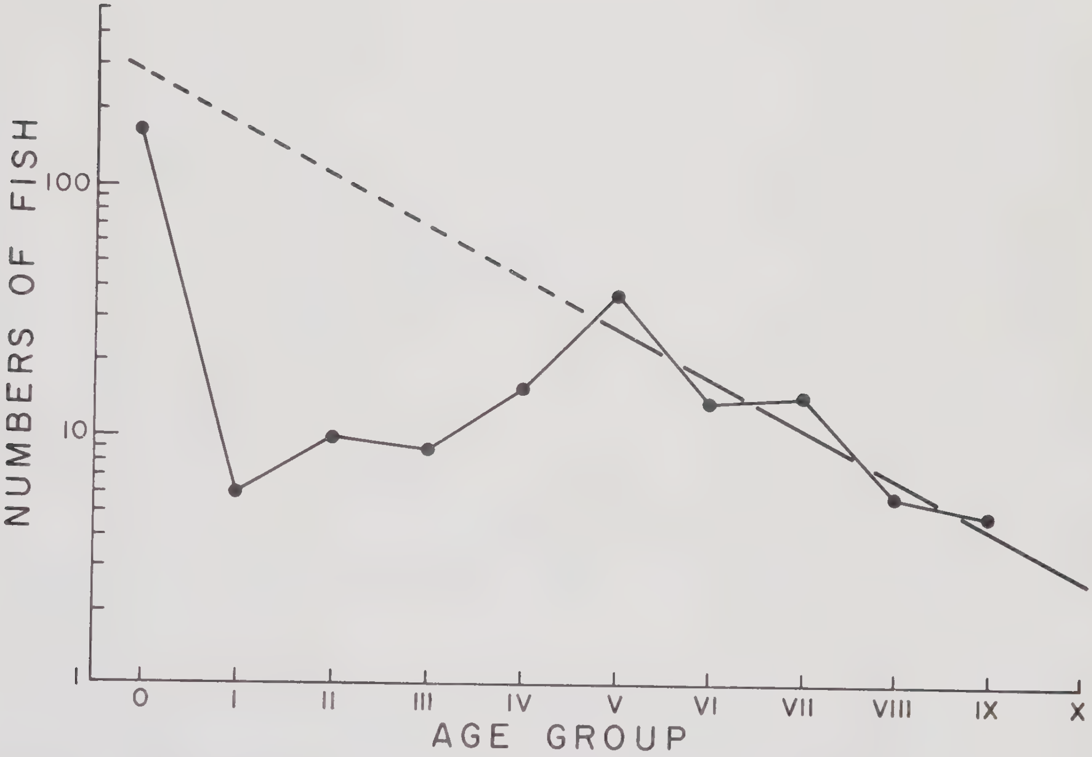


Figure 7.--Catch curve for pile perch captured with otter trawl, seine, and multimeshed gill nets. The trend (heavy line) based on age groups V through IX indicates (dashed portion) expected catches much higher than actually made for age groups I, II, and III.

Testis measurements were made in the field on the unpreserved tissue, the larger of the two gonads being selected for measurement in each case.

Ovaries were fixed in 10 percent formalin and preserved in 40 percent isopropyl alcohol for later examination. Since there was little variation in sizes of normal embryos of a given ovary, average weights were used to describe development of embryos. Average weights were obtained by weighing several embryos together and dividing by the number of embryos weighed. Before weighing, embryo samples were drained in a sieve and the sieve tamped on paper towels to absorb excess moisture. All malformed embryos were recorded but never included in the average weight determinations. These are discussed in detail in the section titled Prenatal Mortality.

To determine egg mortality, 65 ovaries containing embryos were carefully opened and washed out, the wash water decanted, and the sediments searched for eggs under a dissecting microscope. All eggs recovered from these ovaries were recorded and preserved for later study.

Maturity and fecundity

Data from 76 males (fig. 8) indicate that the peak testis index occurred sometime during September and October. The highest index value was observed on September 29 and was about 10 times as large as midsummer values. The gonad index was not applied to age 0 males, but the gonads appeared obviously immature. No conclusions could be made regarding maturity of age I males because none were observed during the mating season.

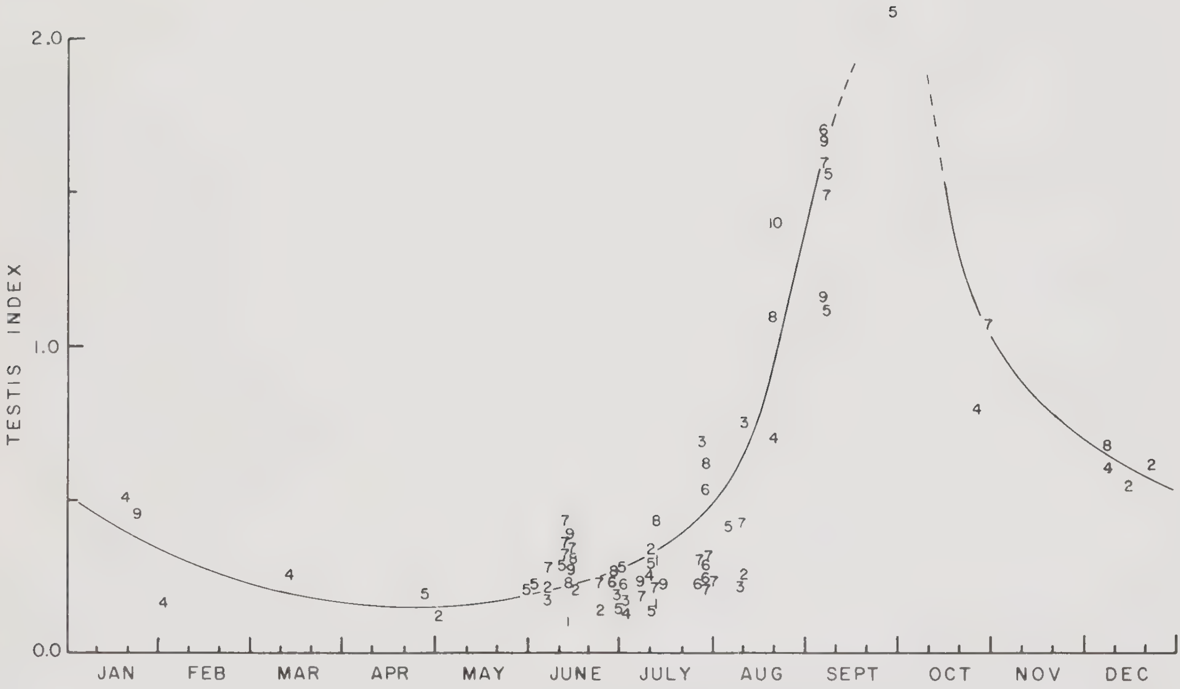


Figure 8.--Seasonal variation in testis index. The index value calculated for each male pile perch is plotted against the date of capture by a number indicating the age of the fish. Trend line fitted by eye.

Index values of two age II males captured in December were three times as great as summertime values, indicating that some may be mature at this age.

In determining age at first maturity, females were considered mature during the year they mated rather than during the year they gave birth. Because data on males indicated fall mating, it was assumed that all gravid females observed in spring or summer months had mated the previous fall. On this basis the earliest maturity was age II, in which 33 percent of 15 specimens were mature. The percentage of females that were mature in each age class is presented in table 1. Caution should be used in applying these percentages to the population in general. There are significant differences in distribution between young and older pile perch, as pointed out in the previous section, and these may be related to sexual maturity. For this reason the sample may be composed of a disproportionately high percentage of mature individuals, and the actual percentage of the population that matures at ages II and III may be considerably less that that indicated.

Table 1.--Maturity of female pile perch [See text for basis of assigning age of maturity]

Age class	Number of females examined	Percent mature
0	42	0
I	2	0
II	15	33
III	35	89
IV	72	97
V or older. .	82	98

Fecundity was positively correlated with size and age of females (fig. 9). The most fecund individual was an age IX female 449 mm TL that contained 61 embryos.

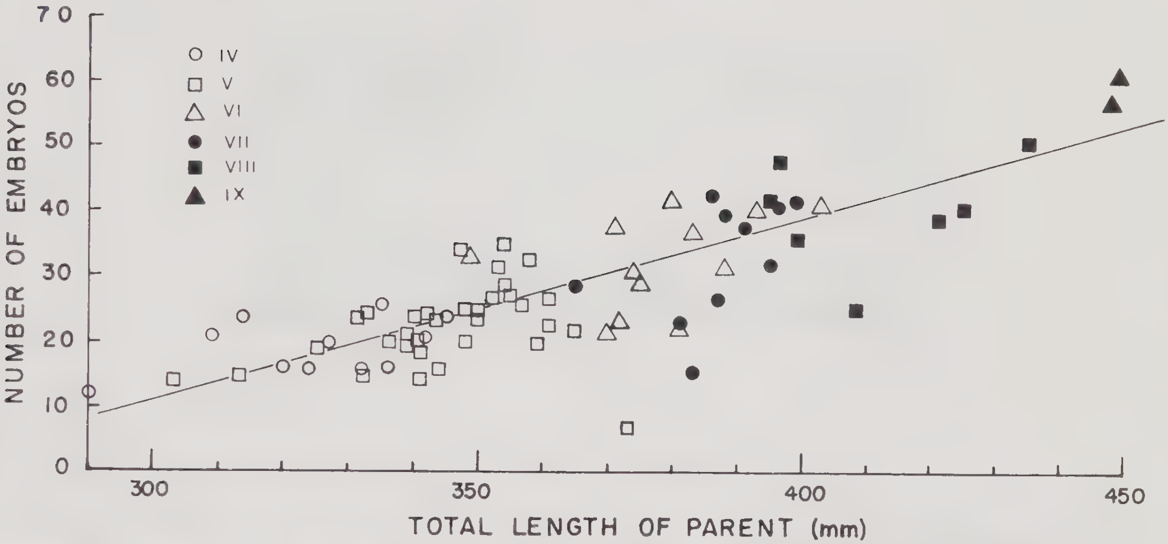


Figure 9.--Length, age, and fecundity relations of 74 pile perch from Yaquina Bay, Oreg., in 1966 and 1967. Trend line fitted by eye. (Only data for which embryos were less than 32 mm SL were included because larger embryos tended to be aborted during capture).

Prenatal mortality

Two sources of prenatal mortality were found: egg deaths and deaths from malformations. Dead eggs were found in ovaries which contained embryos. Many of these eggs were shriveled and opaque, but those in a more normal condition were recognized as fertilized eggs in various stages of development. Since in some cases the embryos occurring with the dead eggs were nearly of terminal size, it appeared that eggs which die before hatching are not resorbed. Therefore, the counts of these eggs may provide valid estimates of mortality between fertilization and hatching. Sixty-five ovaries contained a total of 1,734 embryos and a total of 69 dead eggs, an apparent mortality of 3.8 percent of all eggs fertilized.

Malformed embryos (fig. 10) were considered mortalities because all of the malformations appeared severe enough to be ultimately lethal. It is not known whether any were living at the time of capture, but many obviously were dead and some were partially resorbed. Of 3,699 embryos examined during the study, 44 (1.2 percent) were malformed. Only three ovaries contained more than one malformed individual. In one of these, 19 of 20 embryos were malformed and were about half the size of the normal individual, which was 41 mm SL. All of the malformed embryos in this brood were nearly identical in size and exhibited nearly identical malformations characterized by a tight S-shaped curve (scoliosis) in the anterior portion of the vertebral column. Of 16 embryos in the second ovary, 11 were all less than half the length of the normal embryos but ranged greatly in length (from 6 mm to 11 mm SL). These embryos again were similar to one another in type of malformation, which was characterizeby an enlarged head and protruding lower jaw. The third overy contained three malformed embryos and 29 normal embryos.

Although egg mortality appeared unrelated to age of parent female, occurrence of malformed embryos was markedly associated with younger females (table 2). Females age V or younger carried only 48 percent of all embryos examined but carried 95 percent of all the malformed embryos.

Embryonic growth

Preliminary observations indicated that embryonic growth was essentially exponential. To verify this and to provide a means of

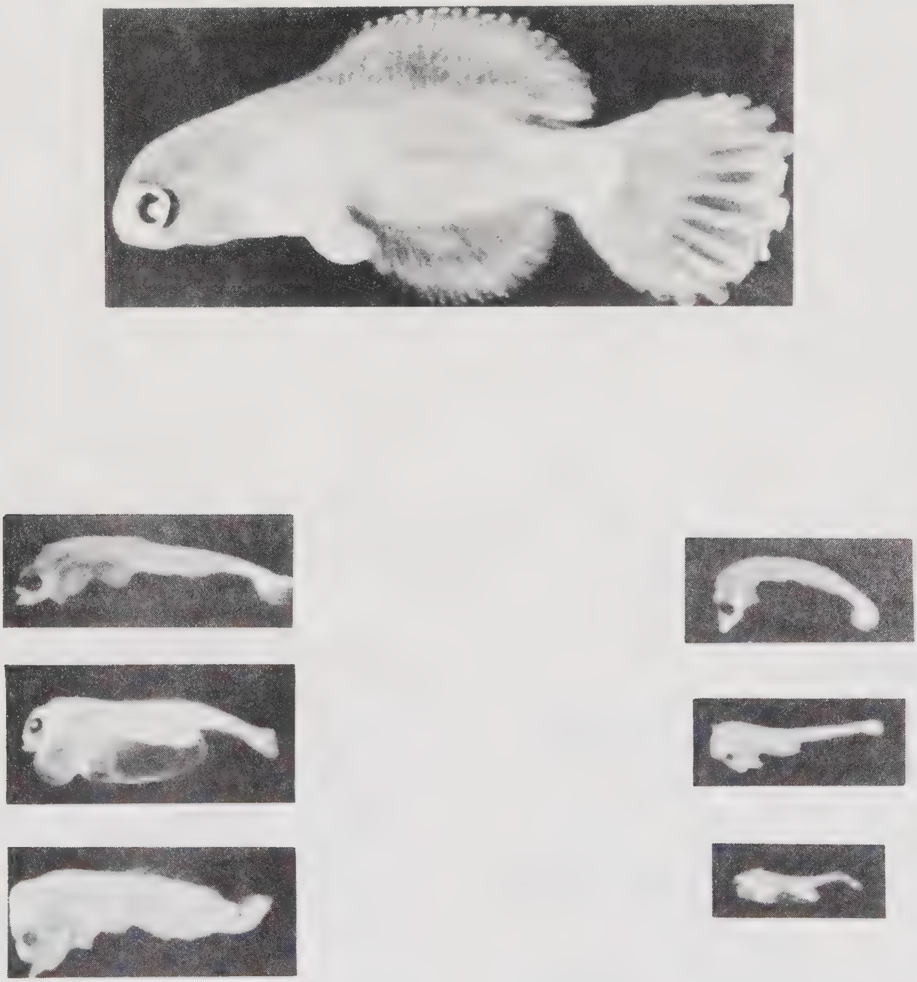


Figure 10.--Normal and malformed pile perch embryos. Standard lengths (mm) of malformed embryos are given, with the average standard lengths of normal embryos from the same ovary shown in parentheses.

extrapolating dates of fertilization and birth, embryo weights were plotted on logarithmic scale against dates of capture (fig. 11). Weight of young at birth and weight of eggs are indicated in the figure by reference lines. Actual average birth weight can be obtained only by holding females in confinement until parturition. In lieu of these data the midpoint, 6.7 g, of the observed range from the smallest newborn (4.5 g) to the largest unborn young observed (8.9 g) was used.

The regression line (A) fitted by least squares to the pooled data for both years had a correlation coefficient (r) of 0.993. The intersections of the regression line with egg weight and birth weight lines indicate that mean fertilization date was January 8 and mean birth date was July 24. This represents a mean gestation period of 196 days. Using the slope of the regression line to project fertilization and birth dates for all the data, it was found that fertilization dates ranged from December 5 to April 25 and birth dates from June 21 to November 12. Ninety percent of the projected fertilization and birth dates were included in the periods December 16 to February 2 and July 1 to August 17 respectively.

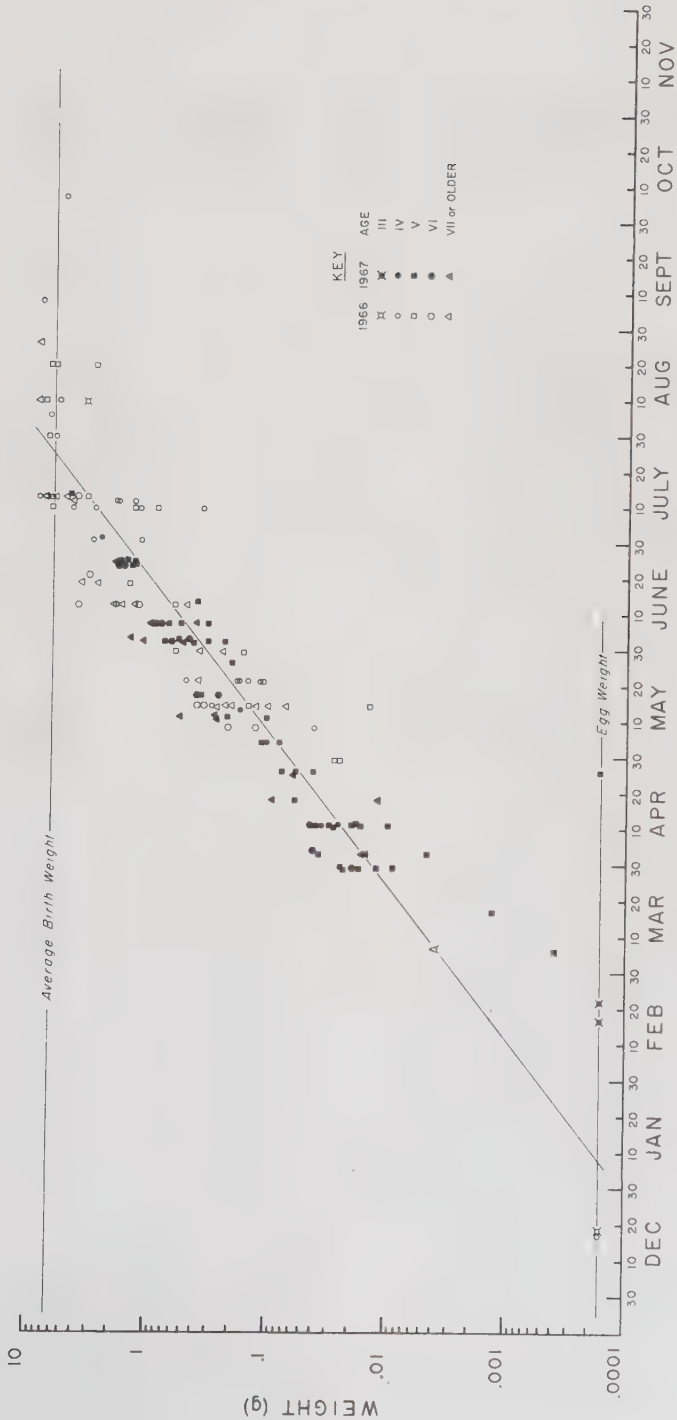


Figure 11.--Weights of fertilized eggs and embryos of pile perch plotted by date of capture and regression line. Symbols indicate age of parent females and year of capture.

Table 2.--Distribution of malformed embryos and dead eggs by age of parent

	For parents in age class--								
	III	IV	V	VI	VII	VIII	IX	X	Total
Embryos:									
Number of ovaries examined	1	27	58	23	18	11	4	1	143
Total number of embryos	24	452	1294	660	569	438	210	52	3699
Number of malformed embryos	0	34	8	1	1	0	0	0	44
Percent malformed	0	7.5	0.6	0.2	0.2	0.0	0.0	0.0	--
Percent of ovaries affected	0	22.2	10.3	4.3	5.5	0.0	0.0	0.0	--
Eggs:									
Number of ovaries examined	0	6	36	10	6	4	3	0	65
Number of embryos plus eggs	--	87	825	361	202	166	162	--	1803
Number of dead eggs	--	2	52	5	3	5	2	--	69
Percent of dead eggs	--	2.3	6.7	1.4	1.5	3.1	1.3	--	--
Percent of ovaries affected	--	33.3	38.9	30.0	33.3	25.0	66.7	--	--

The reproductive cycle may be timed later with increasing latitude because pile perch in southern California are reported to give birth in April (Rechnitzer and Limbaugh, 1952).

Other authors have reported a tendency in some embiotocids for older females to ovulate or to bear young earlier in the season than younger females (Hubbs, 1921; Carlisle, Schott, and Abramson, 1960; Triplett, 1960). Projected birth dates (fig. 12) derived from figure 11 indicate that this generalization would be applicable to pile perch if it could be assumed that size at birth is independent of age (or size) of parent. But the findings of Wilson and Millemann (1969) cast doubt on this assumption. These authors have shown for the shiner perch (Cymatogaster aggregata) that size at birth is directly related to size of parent females--over the range of females they observed, embryo weights ranged from 39 percent below to about 43 percent above the overall average. A similar relation for pile perch would cause an extreme difference in estimated birth dates of about 15 days, which is approximately the difference shown

Delayed fertilization

Eigenmann (1892) demonstrated for the shiner perch (Cymatogaster aggregata) that fertilization occurs about 6 months after mating, and Hubbs (1921) gave evidence which suggests that the reef perch (Amphigonopterus aurora) females also store spermatozoa for a considerable period after mating before the eggs are fertilized. It appears that pile perch females may store sperm for about 3 months before fertilization, since data on males (fig. 8) indicate that mating is centered in late September and data on females (fig. 11) indicate that fertilization is centered in early January.

FOOD HABITS

Methods of analysis

Food habits data were grouped by seasons and by the three zones of Yaquina Bay, giving a combination of 12 "sampling units." The seasons are defined as spring (March-May), summer (June-August), fall (September-

Table 3.--Taxonomic list of all food organisms identified from the stomachs of 190 pile perch collected in Yaquina Bay, Oreg., between April 1966 and July 1967

Phylum Protozoa:	
Class Sarcodina:	
Order Foraminifera	Unidentified Foraminifera
Phylum Annelida:	
Class Polychaeta	Unidentified Polychaeta
Phylum Mollusca:	
Class Gastropoda	Unidentified Gastropoda
Order Archaeogastropoda	*Acmaea* sp.
Order Mesogastropoda:	
Family Calyptraeidae	*Crepidula* sp.
Family Naticidae	Unidentified Naticidae
Order Neogastropoda:	
Family Epitoniidae	Unidentified Epitoniidae
Family Cerithiidae	Unidentified Cerithiidae
Family Olividae	*Olivella biplicata*
Family Muricidae	*Thais canaliculata*
Do	*T. lamellosa*
Order Nudibranchia	Unidentified dorid nubibranch
Class Pelecypoda:	
Order Filibranchia	*Mytilus edulis*
Do	*Ostrea lurida*
Order Eulamellibranchia	Unidentified Eulamellibranchia
Family Tellinidae	*Macoma nasuta*
Do	*M. secta*
Family Cardiidae	*Clinocardium nuttallii*
Family Veneridae	*Protothaca staminea*
Do	*Saxidomus nuttalli*
Do	*Transennella tantilla*
Family Myidae	*Mya arenaria*
Do	*Cryptomya californica*
Family Hiatellidae	*Hiatella* sp.
Family Pholadidae	Unidentified Pholadidae
Phylum Arthropoda:	
Class Crustacea:	
Subclass Cirripedia	*Balanus* sp.
Subclass Malacostraca:	
Order Isopoda	*Idothea* sp.
Order Amphipoda	*Corophium* sp.
Do	Unidentified Amphipoda
Order Decapoda:	
Suborder Natantia	Unidentified Natantia
Suborder Reptantia	*Callianassa californiensis*
Do	*Upogebia pugettensis*
Do	*Pagurus* sp.
Do	*Cancer magister*
Do	*C. productus*
Do	*C. oregonensis*
Do	*Hemigrapsus nudus*
Do	*H. oregonensis*
Do	*Pugettia* sp.
Do	*Pinnixa* sp.
Phylum Echinodermata:	
Class Ophiuroidea	Unidentified Ophiuroidea
Phylum Chordata:	
Class Osteichthyes:	
Order Clupeiformes:	
Family Clupeidae	*Clupea harengus pallasi* (eggs)

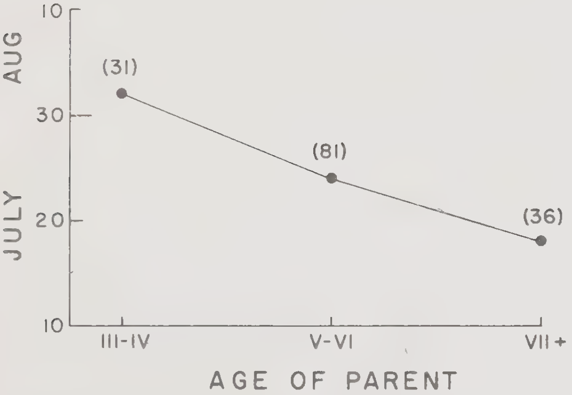


Figure 12.--Mean projected birth dates of embryos by age of parent. Sample sizes in parentheses.

Food habits of young-of-the-year and older fish were treated separately. Both frequency of occurrence and volumetric methods of analysis were used. Frequency of occurrence for each food group is expressed as percent of stomachs containing some food.

The volumetric analysis used for all fish except young-of-the-year was patterned after the method outlined by Reimers (1964), which eliminates bias from differing fish sizes on the assumption that a full stomach is just as important to a small fish as it is to a large one. Stomach capacity was assumed to be proportional to weight of fish, and an adjusted weight-length curve was used to determine potential stomach capacity for each fish. All food volumes were converted to percent of stomach capacity. Since the embiotocid digestive tract is not differentiated into stomach and intestine, the "stomach" was arbitrarily considered as that portion between the pharyngeal teeth and the first bend of the S-shaped digestive tract. Food volumes were measured by water displacement.

Food habits of young-of-the-year perch were analyzed by a different method because of the small size of their stomachs. Separate sample vials were used to preserve the contents from individual digestive tracts or from an aggregate of the digestive tracts collected at the same time and place. The volumetric analysis was based on estimated food fractions of measured total food volumes of samples. In computing frequency of occurrence, each sample was treated as a unit whether it was an aggregate sample or an individual sample.

Young-of-the-year occur only in the summer and fall seasons and were not captured in the lower zone during this study.

Results and discussion

Examinations of 217 stomachs revealed that the fish studied were entirely carnivorous. The traces of plant material occasionally found were usually attached to barnacles or mussels and were probably ingested incidentally. Food was derived from six phyla, but mollusks and arthropods provided 99 percent of the volume in the diet. The food organisms found during the study are listed systematically in table 3. With the exception of crab megalops, all of these animals are typically benthic or sessile. However, crab megalops settle to the bottom just before metamorphosis and are probably captured there rather than in the water column. The bulk of the *Cancer magister* eaten were small, newly metamorphosed individuals.

Frequency of occurrence and volumetric importance of the major stomach contents are presented in figures 13 and 14 grouped as follows: worms (polychaetes), snails (gastropods), mussels (*Mytilus edulis*), clams (all other bivalves), barnacles (*Balanus* sp.), amphipods, mud shrimp (*Upogebia pugettensis*), crabs (true crabs and hermit crabs), megalops (crab megalops larvae), rock, etc. (rock and sand particles).

For a given sampling unit, for both adults and young-of-the-year fish, only a few food species were of importance volumetrically. In all cases the two most important food species made up over 60 percent of the food volume, and with only two exceptions the most important species was at least twice as important volumetrically as any other species (tables 4 and 5). There was a tendency for dominance of diet to shift from encrusting organisms (*Balanus* and *Mytilus*) in the lower zones to mud dwelling organisms (*Protochaca*, *Mya*, and *Upogebia*) in the upper zone.

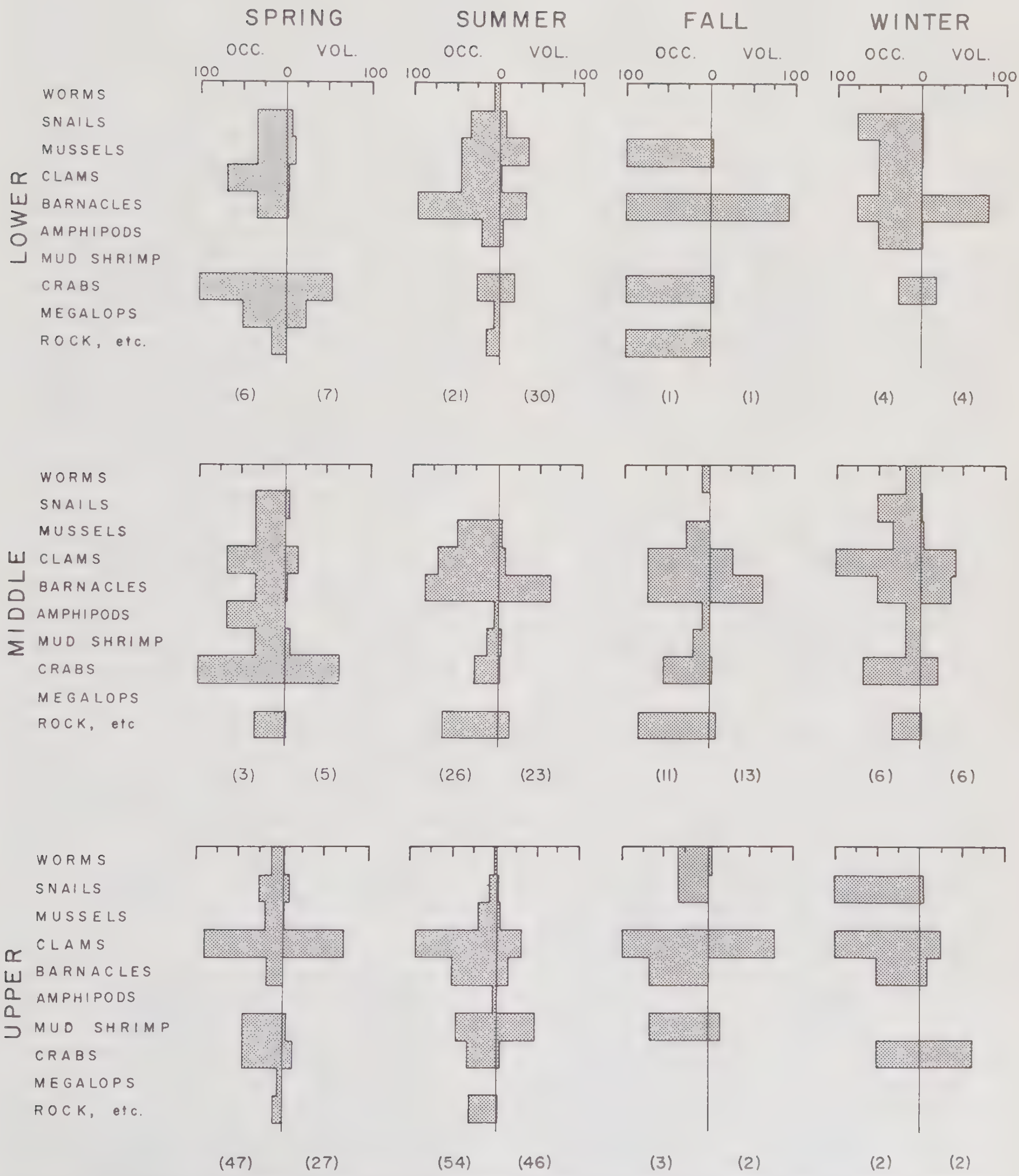


Figure 13.—Seasonal and regional variations in food habits of adult pile perch in Yaquina Bay as percent frequency of occurrence and percent of food volume for major groups of stomach contents. Sample sizes are in parentheses.

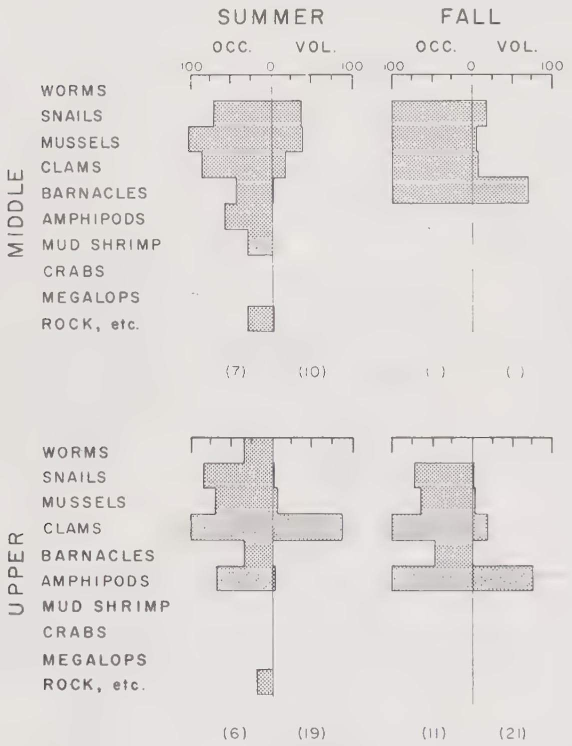


Figure 14.--Seasonal and regional variations in food habits of young-of-the-year pile perch in Yaquina Bay as percent frequency of occurrence and percent of total food volume for major groups of stomach contents. Sample sizes in parentheses refer to numbers of aggregate samples and numbers of fish under occurrence and volume respectively.

The food habits of young-of-the-year differed from those of the older fish by an absence of decapods, little reliance on barnacles, and a significant use of the amphipod *Corophium*, which was not used by adults. They fed on very small individuals (possibly the offspring of the current season) of the same mollusk species as the adults utilized.

Pile perch appear well adapted for the utilization of the hard-shelled animals of the benthos. The strong pharyngeal mill is paved with hard grinding teeth which are calcified even before birth. The undifferentiated tubular shape of the digestive tract and absence of a pylorus may facilitate passage of the great bulk of sharp, angular shell fragments that occur with most of the food organisms. The rectal portion of the digestive tract, which is a darker color than the anterior portion, was prolapsed in many of the specimens captured. Perhaps an ability of the rectum to evert easily is an adaptive mechanism for excretion of abrasive shell fragments.

PARASITES

Methods of study

During the study, 69 pile perch were examined in the laboratory for the presence of

Table 4.--Food organisms, listed in order of importance, which made up 80 percent or more of the food volume of adult pile perch in each sampling unit
[Sample sizes in parentheses]

Zone	Spring		Summer		Fall		Winter	
	Food	Percent	Food	Percent	Food	Percent	Food	Percent
Lower	*C. magister*	51	*M. edulis*	35	*Balanus* sp.	93	*Balanus* sp.	78
	Megalops	23	*Balanus* sp.	33			*C. productus*	18
	M. edulis	11	*C. oregonensis*	12				
	(7)		(30)		(1)		(4)	
Middle	*C. magister*	66	*Balanus* sp.	62	*Balanus* sp.	62	*Balanus* sp.	36
	U. pugettensis	7	*P. staminea*	6	*C. nuttallii*	19	*C. nuttallii*	28
	Cerithidae	6	*M. edulis*	5			*M. nasuta*	11
	M. arenaria	6	*U. pugettensis*	4			*C. productus*	9
			C. magister	3				
	(5)		(23)		(13)		(6)	
Upper	*P. staminea*	48	*U. pugettensis*	45	*M. arenaria*	73	*C. oregonensis*	48
	C. nuttallii	16	*C. californica*	21	*U. pugettensis*	15	*C. nuttallii*	15
	C. magister	9	*Balanus* sp.	16			*C. magister*	12
	C. californica	6					*Balanus* sp.	9
	U. pugettensis	5						
	(27)		(46)		(2)		(2)	

Table 6.--Taxonomic list of parasites identified from the gills, heart, liver, kidney, and digestive tracts of 62 pile perch from Yaquina Bay, Oreg., between June 1966 and July 1967.

Phylum Protozoa:	
Subphylum Cnidosporidea	Unidentified myxosporidian cysts
Phylum Platyhelminthes:	
Class Trematoda:	
Subclass Digenea:	
Family Bucephalidae	*Prosorphynchus* sp.
Do	*Rhipidocotyle* sp.
Do	*Bucephalopsis* sp.
Family Hemiuridae	*Derogenoides* sp.
Family Monochiidae	*Telolecithus pugetensis*
Family Opecoelidae	*Genitocotyle* sp.
Phylum Aschelminthes:	
Class Nematoda:	
Superfamily Spiruroidea	Unidentified spiruroids
Family Cucullanidae	*Cucullanus* sp.
Phylum Arthropoda:	
Class Crustacea:	
Subclass Copepoda:	
Order Caligidea:	
Family Caligidae	*Lepeoptheirus* sp.
Order Lerneopodidea:	
Family Lerneopodidae	*Clavella* sp.

internal parasites. Seven of these were young-of-the-year perch taken in November. At least one adult fish was autopsied each month. The digestive tract, heart, liver, spleen, kidney, and gills were checked.

A stereoscopic (X7 to X30 variable power) microscope was used to search for parasites. The digestive tract was slip open and examined while a stream of water from a squeeze bottle was played over its internal surface. When excessive amounts of slime adhering to the mucosa prevented this method, the tissue was shaken vigorously in a jar of tap water and reexamined. Any parasites in the wash water were recovered by settling and decanting. Each gill arch was examined for external parasites; the other organs were teased apart carefully to find parasites imbedded in the tissues as well as those on the surface. Infestation rates were calculated by dividing the number of parasites found by the number of fish examined.

Results and discussion

The parasites found infecting pile perch are listed systematically in table 6.

The only parasite infecting young-of-the-year fish was the copepod *Clavella* sp., attached to the ends of the gill filaments. The average infestation in these young fish was 2.4 parasites per fish; the most heavily infected fish had seven parasites.

Adult fish had more parasites than young-of-the-year fish. Of 45 adult pile perch, 13 were infected with myxosporidian cysts on the gills. These had an average of 17 cysts per fish, and the most heavily infected fish carried 99 cysts. Three adult trematodes of the genus *Derogenoides* and four immature spiruroid nematodes were found in the livers. One adult specimen each of the trematodes *Telolecithus pugetensis* and *Genitocotyle* sp.

and 10 adult nematodes (Cucullanus sp.) were found in the digestive tracts.

Of the two species of copepods found in the gills, Clavella sp. was more abundant than Lepeoptheirus sp. For both species, infestation rates were markedly greater during summer and fall than winter and spring (fig. 15). This seasonal trend held for perch sampled in each zone of the Bay, although there was also a tendency for infestations of Clavella sp. to be higher in the upper zone during each season. Extent of copepod infections was clearly not related to size of fish.

Of 47 perch, 17 were infected with encysted metacercariae of bucephalid trematodes belonging to the genera Prosorhychus, Rhipidocotyle, and Bucephalopsis. The minute cysts of these parasites were found in the heart, liver, and kidney, with infestation rate directly related to fish size (fig. 16), suggesting that these cysts are accumulated over the years.

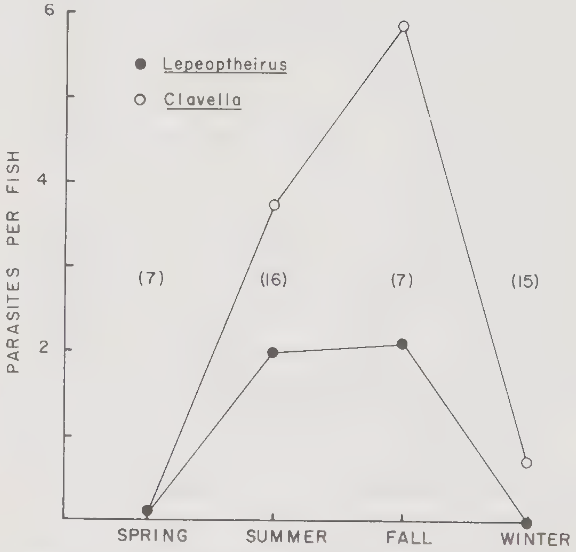


Figure 15.--Infestation rates of gill copepods by seasons. Number of pile perch sampled in each season is given in parentheses.

None of the parasite infections appeared to have been significant to the health of the host pile perch, though slight mechanical damage to gill filaments from copepods was noted.

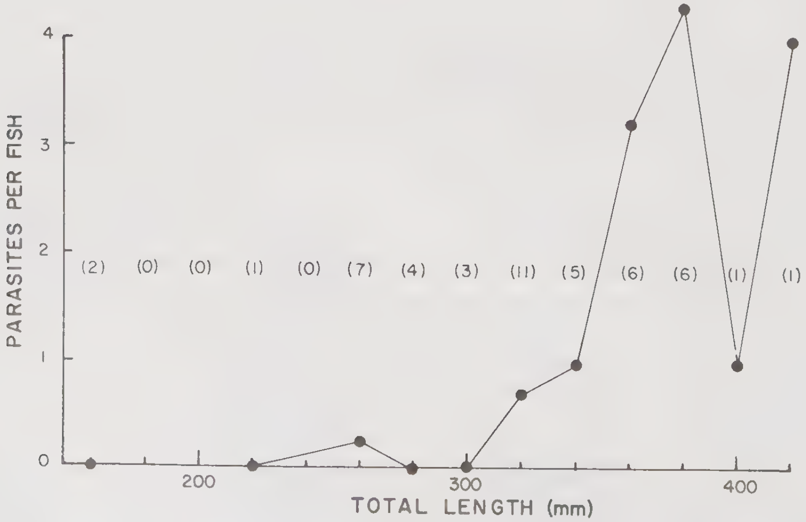


Figure 16.--Infestation rate of bucephalid metacercariae in the heart, liver, and kidney as a function of fish length. Numbers of pile perch sampled in each 20 mm length group are given in parentheses.

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DISTRIBUTION, APPARENT ABUNDANCE, AND LENGTH COMPOSITION OF JUVENILE ALBACORE, *Thunnus alalunga*, IN THE SOUTH PACIFIC OCEAN

HOWARD O. YOSHIDA[1]

ABSTRACT

The distribution, apparent abundance, and length composition of juvenile albacore, *Thunnus alalunga*, were deduced from 127 specimens found in the stomachs of 2,297 billfishes collected in the South Pacific between January 1964 and July 1966. Juvenile albacore were found in the South Pacific from lat 5° to 31° S, between long 153° and 179° W. Billfish stomach samples were collected from as far east as long 135° W, but juveniles were not in the stomachs east of long 153° W. The juveniles were consistently more numerous between lat 10° and 20° S than in the area farther north. The mean length of the juveniles increased from north to south but not from east to west (or vice versa). A southward migration of juveniles is postulated.

In April 1963, the National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries), Hawaii Area Fishery Research Center established a field station in Pago Pago, American Samoa, to collect information on the longline fishery based there. A fleet of vessels from Japan, the Republic of Korea, and the Republic of China has supplied two American-owned canneries with albacore, *Thunnus alalunga*, and other tuna. In 1965 the fleet was composed of 154 vessels which landed 15,588 metric tons of albacore (Otsu and Sumida, 1968).

The field station was established primarily to study the effects of the fishery on albacore. As part of this study an investigation was started to determine the early life history of albacore in the South Pacific.

Beginning in 1964, arrangements were made with several longline fishing vessels based in American Samoa to collect stomachs of billfishes, which are known to prey on juvenile tunas (Yoshida, 1965, 1968). The distribution, apparent abundance, and length composition of juvenile albacore, here defined as fish smaller than 400 mm standard length, were determined by specimens found in the stomachs of the predators.

MATERIALS AND METHODS

The longline vessels based at American Samoa fished primarily for albacore; billfishes were taken only incidentally. The crews of the cooperating longline vessels collected 2,297 billfish[2] stomachs between January 1964 and July 1966. These stomachs were also used in a study of juvenile skipjack tuna, *Katsuwonus pelamis* (Yoshida, 1971).

In the laboratory, all the tunas and tunalike specimens were first sorted from the stomach contents. The juvenile tunas were identified by the use of skeletal characters; juvenile albacore were easily identified by their definitive skeletal characters (Matsumoto, 1963; Yoshida, 1965). Standard length (SL) was taken for all intact juveniles and is the measurement used throughout. For fragmentary specimens, the standard length was estimated from previously determined relations between standard length and various vertebral segments (Yoshida, 1968). A total of 127 juvenile albacore was found in the billfish stomachs (Table 1).

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[2] For the purpose of this paper the term billfish, in addition to the Istiophoridae, includes the swordfish, *Xiphias gladius*.

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TABLE 1.—Juvenile albacore found in billfish stomachs from the South Pacific.

Date 1964	Position		Standard length	Date 1965	Position		Standard length	Date 1966	Position		Standard length
	Lat S	Long W			Lat S	Long W			Lat S	Long W	
			mm				*mm*				*mm*
3/9	07°00′	170°00′	143	1/5	14°00′	174°00′	122	1/7	15°00′	175°00′	107
3/20	06°00′	164°00′	116	1/5	14°00′	174°00′	97	1/9	15°00′	174°00′	89
3/21	05°00′	165°00′	67	1/22	14°00′	175°00′	96	1/9	15°00′	174°00′	83
4/4	08°00′	175°00′	102	1/22	14°00′	175°00′	78	1/9	16°00′	174°00′	110
4/5	08°00′	175°00′	136	1/22	14°00′	175°00′	84	1/9	16°00′	174°00′	113
4/9	07°00′	178°00′	78	1/24	14°00′	174°00′	102	1/9	16°00′	174°00′	133
4/9	07°00′	178°00′	137	1/25	14°00′	174°00′	109	1/17	12°00′	175°00′	106
4/12	07°00′	178°00′	26	1/26	11°00′	162°40′	81	1/23	12°40′	171°00′	133
4/16	07°00′	179°00′	57	1/27	14°00′	174°00′	118	2/8	09°00′	172°00′	130
4/19	07°00′	178°00′	102	1/29	14°00′	175°00′	110	2/8	09°00′	172°00′	137
4/20	07°00′	179°00′	66	1/30	14°00′	175°00′	102	2/8	09°00′	172°00′	130
4/20	07°00′	179°00′	66	4/4	07°10′	164°13′	123	2/8	09°00′	172°00′	93
4/20	07°00′	179°00′	106	4/12	07°10′	170°20′	102	2/13	07°02′	171°30′	102
4/24	09°00′	176°00′	115	4/22	07°00′	174°45′	86	3/7	06°35′	162°20′	58
4/25	08°00′	176°00′	67	4/22	07°00′	174°45′	86	3/14	07°20′	161°15′	89
4/26	08°00′	177°00′	119	9/1	13°00′	171°00′	96	3/16	08°10′	165°13′	67
5/8	07°54′	165°32′	118	11/7	16°30′	159°20′	152	3/22	11°32′	168°29′	104
5/3	07°54′	165°32′	113	11/7	16°30′	159°20′	158	3/22	11°32′	168°29′	116
5/8	07°54′	165°32′	104	11/7	16°30′	159°20′	142	3/28	09°10′	153°00′	168
5/8	07°54′	165°32′	113	11/8	16°20′	159°09′	152	5/5	08°13′	175°42′	83
5/8	07°54′	165°32′	88	11/22	17°00′	168°00′	105	5/5	08°13′	175°42′	92
5/8	07°54′	165°32′	106	11/29	17°07′	170°43′	119	5/5	08°13′	175°42′	97
5/8	07°54′	165°32′	125	11/29	17°07′	170°43′	115	5/7	08°00′	175°45′	94
5/10	07°46′	165°29′	121	11/29	17°07′	170°43′	91	5/9	08°28′	175°57′	53
5/10	07°46′	165°29′	88	12/14	17°50′	159°30′	137	6/8	07°15′	164°42′	74
5/19	05°29′	170°06′	48	12/14	17°50′	159°30′	148	6/29	30°49′	166°13′	314
5/19	06°00′	172°00′	47	12/17	16°11′	157°27′	100	7/12	28°50′	156°03′	297
5/23	06°00′	173°00′	58	12/21	17°52′	158°20′	138	7/15	28°05′	155°24′	317
5/26	06°23′	173°59′	99	12/22	10°00′	174°00′	159	7/23	28°44′	154°15′	321
6/1	05°52′	174°41′	48	12/25	18°00′	163°00′	130	7/23	28°44′	154°15′	316
6/1	05°52′	174°41′	73	12/25	18°00′	163°00′	164	7/24	28°22′	154°24′	301
6/20	06°43′	171°26′	53	12/28	17°30′	162°10′	162				
6/25	07°18′	172°53′	86	12/29	12°00′	171°00′	93				
8/18	26°00′	175°00′	357	12/30	12°00′	171°00′	115				
8/21	26°00′	176°00′	358	12/31	12°00′	171°00′	93				
9/4	24°00′	174°00′	328								
9/5	25°00′	174°00′	343								
9/9	25°00′	171°00′	333								
9/9	25°00′	171°00′	301								
9/13	18°00′	170°00′	230								
9/13	18°00′	170°00′	230								
9/13	18°00′	170°00′	223								
9/19	16°00′	173°00′	110								
10/4	09°00′	179°00′	93								
10/4	09°00′	179°00′	116								
10/4	15°00′	173°00′	93								
10/8	19°00′	173°00′	146								
10/9	17°00′	173°00′	185								
10/18	13°00′	174°00′	62								
10/22	15°00′	174°00′	83								
10/22	15°00′	174°00′	93								
10/22	15°00′	174°00′	78								
11/11	16°00′	171°00′	79								
11/13	16°00′	171°00′	62								
11/13	16°00′	171°00′	128								
11/14	16°00′	171°00′	133								
11/15	16°00′	175°00′	150								
11/16	16°00′	172°00′	110								
11/16	16°00′	172°00′	150								
12/18	14°00′	174°00′	102								
12/31	14°00′	175°00′	133								

LENGTH OF JUVENILES

The juvenile albacore in the billfish stomachs ranged from 26 to 358 mm (Figure 1). Two length groups were apparent in the length-frequency distribution: one with a mode at 110 mm and the other at 310 mm; another length group was suggested between 200 and 250 mm.

In the course of the study it became apparent that the larger juveniles were being taken between lat 20° and 30° S. To determine if differences existed in juvenile sizes by latitude, lengths were plotted against latitude of capture (Figure 2). The smallest individuals were taken north of lat 10° S and the largest south of lat 20° S. No specimens smaller than 290 mm were taken south of lat 20° S. The juveniles between lat 10° and 20° S were slightly larger (mean SL 120 mm) than those taken north of lat 10° S (mean SL 94 mm). The mean standard length of those from south of lat 20° S was 324 mm.

In contrast to the latitudinal differences in juvenile length, no longitudinal trends in length were evident. Juveniles larger than 300 mm were taken in the eastern as well as the more westerly portion of the area sampled.

MIGRATION OF JUVENILES

The differences in the lengths of the albacore in the three latitudinal bands may be caused by the migration of the juveniles. The increase in length of juveniles from north to south and the absence of any longitudinal trends in length suggest a southward migration. After attaining a length of nearly 200 mm the juveniles that originate between the equator and lat 10° S probably start migrating south. They apparently continue to move southward as they grow. This migration would explain the absence of large (>250 mm) juveniles north of lat 20° S.

These observations on the suspected migration pattern of juvenile albacore fit well with the accumulated information on the biology of albacore in the South Pacific. Observations on the length composition of commercial catches of albacore in the South Pacific indicate latitudinal differences in the size of albacore. Adult albacore tend to be small north of lat 15° S and largest between lat 20° and 25° S. They are smaller again south of lat 25° S (Otsu and Sumida, 1968). Length-frequency data published by the Nankai Regional Fisheries Research Laboratory (1959) show that albacore as small as 490 to 500 mm are caught on longlines south of lat 30° S. Thus, it could be that the juveniles move southward as they grow and are first taken by the longline fishery as preadults in the higher latitudes in the South Pacific. A similar pat-

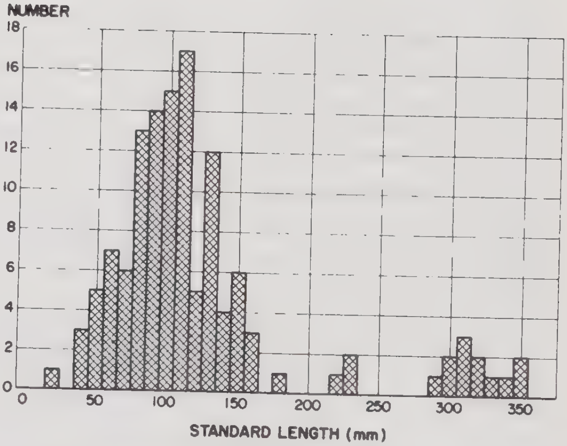

FIGURE 1.—Length-frequency distribution of juvenile albacore in the South Pacific.

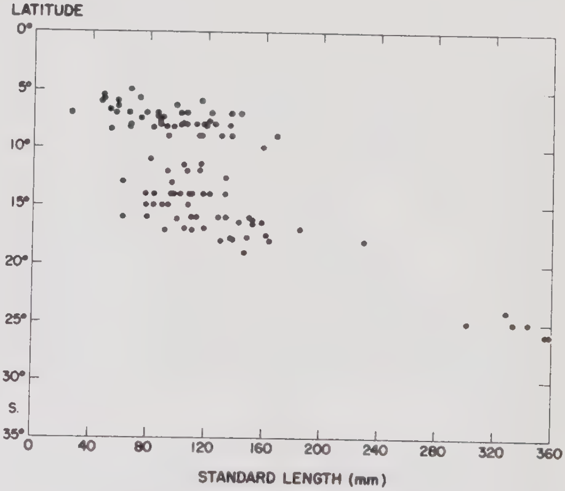

FIGURE 2.—The length of juvenile albacore plotted against latitude of capture.

tern has been deduced for albacore in the North Pacific. Otsu and Uchida (1963) hypothesized that the juveniles in the North Pacific migrate from tropical and subtropical waters into temperate waters and are recruited into the adult population in higher latitudes, presumably north of lat 30° N. Generally speaking, then, the albacore in the North and South Pacific, which are believed to constitute separate subpopulations, follow similar migration patterns within their respective hemispheres. The adults are believed to spawn in lower latitudes, between the equator and lat 20° where the eggs hatch and the larvae develop into juveniles. The juveniles then migrate into higher latitudes as they grow and they join the adult population in the higher latitudes.

AGE AND GROWTH

Information on age and growth is useful in determining certain vital statistics for fish populations and it would be useful if the growth of juvenile albacore in the South Pacific could be determined. Around Hawaii juveniles (60-350 mm SL) were estimated to grow about 31 mm per month (Yoshida, 1968). It would have been interesting to compare this growth with that of juveniles in the South Pacific. A plot of juvenile albacore length by time of capture, however, did not indicate that the length of the juveniles was increasing with time.

DISTRIBUTION AND ABUNDANCE

Because the data for any one year were sparse, the data for all years were combined to determine the quarterly distribution of juvenile albacore (Figure 3). The apparent distribution of juvenile albacore may reflect the operations of the longline boats. The longline vessels based at American Samoa primarily were seeking albacore and selecting areas where albacore catch rates tended to be high. The vessels generally fished north of lat 20° S in the first half of the year and beginning in June or July moved southward to as far south as lat 30° S (Otsu and Sumida, 1968). The data indicated that the cooperating vessels generally followed this pattern. In spite of this shortcoming the data suggest some interesting features of the seasonal distribution of juvenile albacore.

In the first quarter billfish stomach samples were collected between long 150° and 178° W and lat 5° and 16° S. The juveniles were generally found throughout the sampling area west of long 153° W.

In the second quarter the longitudinal range of sampling was slightly greater but the juveniles were restricted to the west between long 165° and 179° W. Latitudinally, most of the stomach samples were from north of lat 10° S except for a few samples from about lat 31° S. Juveniles were taken between lat 5° and 9° S and at lat 31° S.

In the third quarter stomach samples were available from long 140° W to 178° E between lat 5° and 31° S. The juveniles were absent in samples from north of 14° S.

In the fourth quarter the sampling area was bounded by long 135° W and 178° E and lat 6° and 21° S. Juveniles were absent from the easternmost portion of the area. They were taken between long 157° and 179° W and lat 9° and 20° S. These observations suggest that the center of the spawning area is closer to the area between long 160° W and the 180th meridian than farther to the east.

Variations were also evident in the apparent abundance of juvenile albacore as indicated by the number of juveniles found monthly per 100 billfish stomachs (Figure 4).

Juvenile albacore were found in all months except July and August. Peaks in apparent abundance occurred in January, April, and November.

The data for all years were pooled because billfish stomachs were unavailable for some months in some years. Also, estimates of apparent abundance may be biased by the small sample sizes. The shortcoming of combining data for all years and considering a large area as an entity is that annual and areal variations in apparent abundance are obscured. For example, in 1965, except in April when four juvenile albacore were taken, no juveniles were found in billfish stomachs from north of lat 10° S.

The overall abundance of juveniles was greater

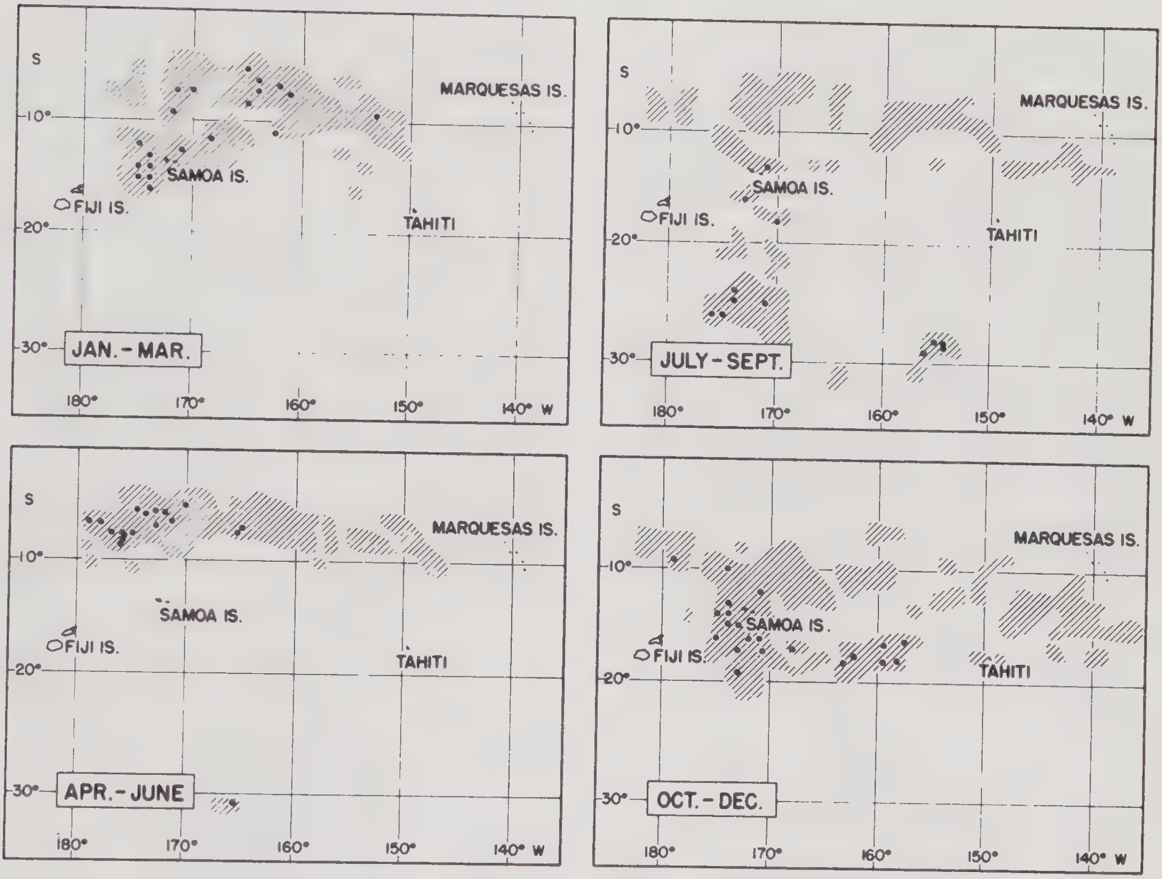

FIGURE 3.—The quarterly distribution of juvenile albacore in the South Pacific, all years combined. The shadings show areas from which billfish stomachs were collected. The dots show where juvenile albacore were taken.

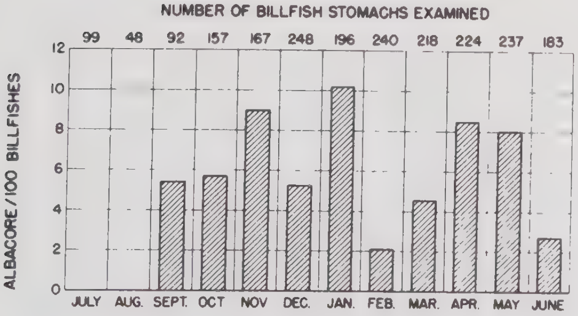

FIGURE 4.—Apparent abundance of juvenile albacore in the South Pacific.

between lat 10° and 20° S than in the area north of lat 10° S. Combining the data for all years, 7.5 juveniles per 100 billfishes were taken between lat 10° and 20° S, and 4.5 juveniles per 100 billfishes were taken north of lat 10° S. (Near Hawaii between July 1962 and April 1966, juvenile albacore were taken at a rate of 0.8 per 100 billfishes [Yoshida, 1968]. Thus, juvenile albacore are apparently more numerous in the South Pacific than around Hawaii.)

SPAWNING

Variations in seasonal and geographic distribution and apparent abundance of juvenile albacore may be related to the spawning of the adults. Several investigators have made observations on the spawning of albacore in the South Pacific. On the basis of an examination of ovaries, Otsu and Hansen (1962) concluded that peak albacore spawning occurs in the southern hemisphere summer between the equator and lat 20° S. Their results also suggest a spawning season of at least 5 months. Ueyanagi (1969), who based his study on the distribution of larvae and on the stage of maturity of ovaries of adults, also suggested a southern summer spawning season. The seasonal apparent abundance of juvenile albacore does not disagree with the above conclusions. The fact that juveniles were found in all but 2 months of the year suggests a long spawning season. The presence of juvenile albacore during and beyond the southern hemisphere summer indicates some spawning during the summer. My data also suggest annual variations in adult spawning. The virtual absence of juvenile albacore north of lat 10° S in 1965 indicates little or no spawning in this area during that year.

COMPARISON WITH SKIPJACK TUNA

A comparison of the distribution and abundance of juvenile albacore and skipjack tuna offers some interesting contrasts. Although billfish stomachs were sampled from long 135° W to 177° E, juvenile albacore were found only between long 153° and 179° W (Figure 5). The juveniles were found throughout the latitudinal range of sampling between lat 5° and 31° S. Juvenile skipjack tuna are distributed over a wider area: between long 137° W and the 180th meridian from lat 5° to 32° S (Yoshida, 1971). These distributional patterns indicate that skipjack tuna spawn over a wider area than the albacore in the South Pacific.

Comparing the abundance of the two species, in 1964 juvenile skipjack tuna were more numerous north of lat 10° S than from 10° to 20° S, but in 1965 they were more numerous between 10° and 20° S than in the area to the north (Yoshida, 1971). Juvenile albacore were consistently more abundant between lat 10° and 20° S than to the north. Also, juvenile skipjack tuna apparently were from 4.5 to 15 times more numerous than juvenile albacore between the equator and lat 20° S (Table 2). It is also interesting that the apparent abundance of both species declined from 1964 to 1965.

TABLE 2.—Apparent abundance of juvenile albacore and skipjack tuna in the South Pacific. The apparent abundance is expressed as number per 100 billfishes. Data for juvenile skipjack tuna are from Yoshida (1971).

Year	North of lat 10° S		Lat 10°-20° S	
	Albacore	Skipjack tuna	Albacore	Skipjack tuna
1964	6.7	46.3	9.3	42.6
1965	1.9	28.8	5.8	35.6

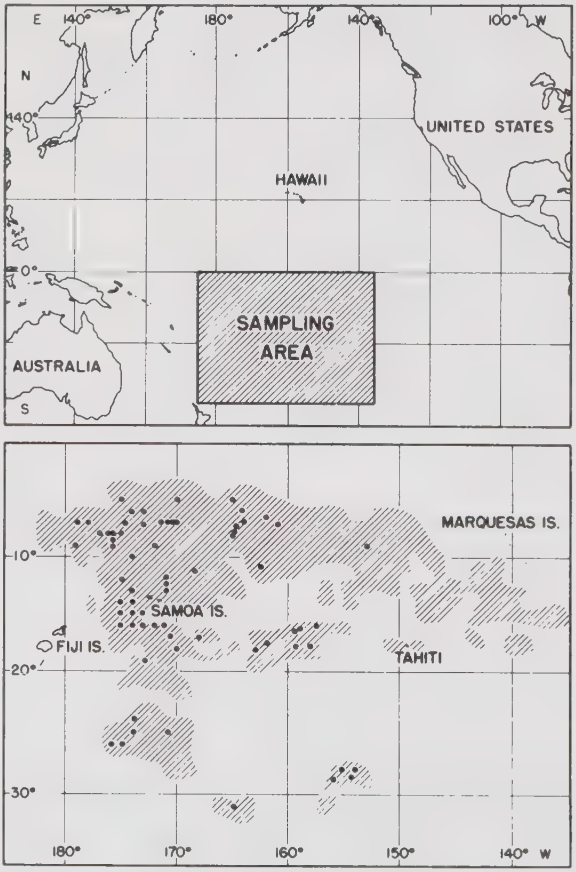

FIGURE 5.—The distribution of billfishes (shading) sampled by the cooperating longline vessels and the distribution of juvenile albacore (dots) found in the billfish stomachs.

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THE EARLY LIFE HISTORY OF SKIPJACK TUNA, *Katsuwonus pelamis,* IN THE PACIFIC OCEAN

Howard O. Yoshida[1]

ABSTRACT

This study investigates the early life history of skipjack tuna, including the distribution, abundance, age, and growth. The study is based on 1,742 juvenile skipjack tuna that were found in the stomachs of 6,867 billfishes caught in Hawaiian waters and in the South Pacific by commercial longline boats. The smallest juvenile taken near Hawaii was 5.9 cm in standard length, and in the South Pacific 1.6 cm in standard length. Regressions describing the relations between the standard length and lengths of (1) the vertebral column, (2) the precaudal vertebrae, (3) caudal vertebrae, (4) the 1st-10th vertebrae, and (5) the 21st-30th vertebrae of juvenile skipjack tuna were determined. The regressions provided estimates of the standard length of fragmentary specimens. Juvenile skipjack tuna were widely distributed between lat 5° and 32° S, and long 137° W and the 180th meridian. North of the equator, the commercial longline boats fished close to the main Hawaiian Islands, and thus only a limited picture was obtained of the areal distribution of juvenile skipjack tuna. Juvenile skipjack tuna were found in almost all months in Hawaiian waters. They were most numerous in July and August. In the South Pacific, juveniles were also found in almost all months between lat 5° and 20° S. Peaks in the apparent abundance were evident in April and October in the area north of lat 10° S. Juvenile skipjack tuna appeared to be more numerous in the South Pacific than around Hawaii.

Length-frequency distributions of juvenile skipjack tuna from Hawaii showed well-defined modes, which progressed with time. The growth of the juveniles was estimated by using the modal lengths determined from the monthly length-frequency distributions. Skipjack tuna between 9 and 40 cm around Hawaii are estimated to grow 2.0 cm per month. One-year-old fish are estimated to be 31 cm in standard length.

In 1968, 70,746 metric tons of skipjack tuna, *Katsuwonus pelamis,* were landed in the eastern Pacific (Inter-American Tropical Tuna Commission, 1970) and 109,018 metric tons were landed in Japan (Japan. Fisheries Agency, Research Division, 1970). Because of its commercial importance much knowledge has been accumulated on the biology of the skipjack tuna. Information on early life history, however, is incomplete. Matsumoto (1958) described skipjack tuna larvae and their temporal and spatial distribution in the central Pacific. Ueyanagi (1969) reported on the distribution of larval skipjack tuna in the Pacific Ocean between 1960 and 1967, and Higgins (1967) summarized the distributional records of juvenile skipjack tuna in the Pacific.

The present study is based on immature skipjack tuna between 1.6 and 40 cm taken from the stomachs of billfishes near Hawaii and in the South Pacific. Included are observations on geographical and seasonal distribution, length-frequency distributions, and age and growth rates.

MATERIALS AND METHODS

The stomachs of 6,867 billfishes[2] were examined in this study. Those examined included 4,118 striped marlin, *Tetrapturus audax;* 1,606 blue marlin, *Makaira nigricans;* 383 shortbill spearfish, *T. angustirostris;* 216 sailfish, *Istiophorus platypterus;* 196 swordfish, *Xiphias gladius;* 171 black marlin, *M. indica;* and 177 billfishes that were not identified to species.

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[2] The term billfishes as used in this paper includes swordfish.

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Sixty-six percent of the stomachs came from billfishes captured near Hawaii between July 1962 and April 1966. These stomachs were used previously in an early life history study of albacore, *Thunnus alalunga* (Yoshida, 1968). Most of these billfishes were caught within 37 km (20 nautical miles) of the main islands. A few were caught as far as 740 km (400 nautical miles) from Oahu. Thirty-four percent of the stomachs came from billfishes caught in the South Pacific between lat 5° and 32° S, and between long 135° W and 179° E (Figure 1). These were caught on longline gear by boats operating out of American Samoa between January 1964 and July 1966. The fishery has been described by Otsu and Sumida (1968).

Arrangements were made with the crews of several boats to have billfish stomachs collected on the fishing voyages. Each cooperating crew was provided with a stainless steel tank, formaldehyde solution, labels, and collecting bags. The crew was paid 50 cents for each stomach.

In the laboratory at Honolulu, all tuna and tunalike specimens were sorted from the stomach contents and identified. Skipjack tuna were identified by skeletal characters (Godsil and Byers, 1944). Standard length was recorded for all intact specimens. Following a technique used earlier (Yoshida, 1968), a method was devised to estimate the standard length of fragmentary specimens. Relations were determined between the standard length and the length of: (1) the complete vertebral column (41 vertebrae), (2) the precaudal vertebrae (vertebrae 1-20), (3) the caudal vertebrae (vertebrae 21-41), (4) 1st-10th vertebrae, and (5) 21st-30th vertebrae, based on 77 intact juvenile skipjack tuna specimens from around Hawaii and the South Pacific. All the relations appeared to be linear and straight lines were fitted to the data by the method of least squares. Combining the samples from Hawaii and the South Pacific should not adversely affect the results. A plot of the data for all five relations did not indicate any differences between the North Pacific and South Pacific samples. A covariance analysis applied to the relation between the standard length and the length of the complete vertebral column for Hawaiian and South Pacific juvenile skipjack tuna confirmed the lack of significant differences between the samples. No significant differences were found in the regression coefficients ($F = 0.105$; df = 1, 73) and in the intercepts ($F = 0.053$; df = 1, 74). The regressions of the standard length on the various vertebral segments are presented in Table 1.

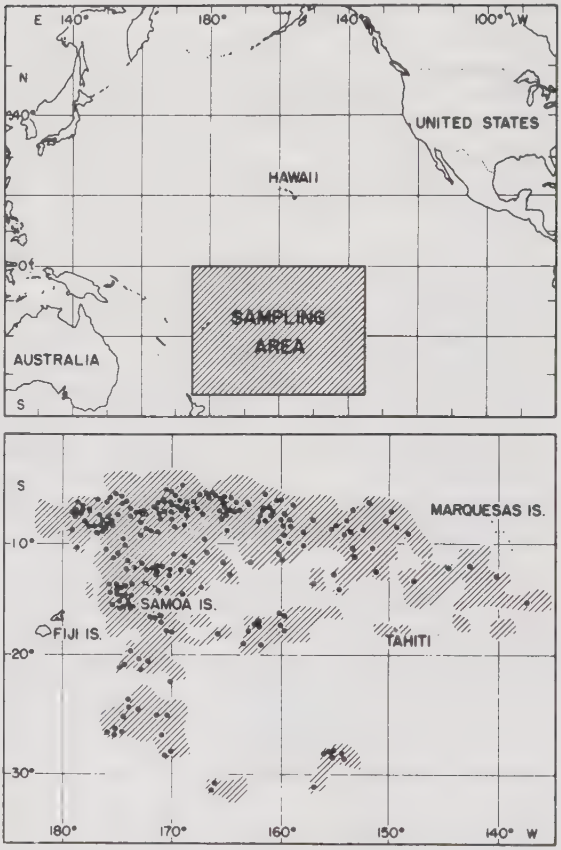


FIGURE 1.—The location of capture of billfishes (shaded area) and the distribution of juvenile skipjack tuna (dots) in the South Pacific.

The lengths of most of the specimens were estimated by using a suitable regression. For 22% of the specimens the relative position of the fragments could not be determined, and the regressions were not used. For these specimens the standard length was estimated by comparing the average length of the vertebrae in the fragment with the average length of the vertebrae of the specimens used to calculate the regressions.

TABLE 1.—Regressions describing the relations between the standard length and lengths of the vertebral column, precaudal vertebrae, caudal vertebrae, 1st-10th vertebrae, and 21st-30th vertebrae of juvenile skipjack tuna [l = standard length (cm), L = length of vertebral fragments (cm)].

Segment of vertebral column	Regression	Standard deviation from regression
Complete vertebral column	$l = 0.0693 + 1.2262L$	0.435
Precaudal vertebrae	$l = 0.6544 + 2.4926L$	0.439
Caudal vertebrae	$l = -0.4414 + 2.4196L$	0.445
1st-10th vertebrae	$l = 0.4280 + 5.2938L$	0.515
21st-30th vertebrae	$l = -0.2637 + 4.6942L$	0.595

DISTRIBUTION AND ABUNDANCE

Seasonal and areal coverage was spotty, but sampling was extensive enough to permit meaningful analysis for the present study. In the following sections I will discuss the distribution and the seasonal and annual apparent abundance of juvenile skipjack tuna in the South Pacific and near Hawaii.

AREAL DISTRIBUTION

Commercial longline boats engaged in collecting billfish stomachs in the South Pacific ranged over a wide area, and juvenile skipjack tuna, as indicated by their presence in billfish stomachs, also were widespread (Figure 1). Around Hawaii fishing was restricted to a relatively small area, and so a more limited picture was obtained of the areal distribution of juvenile skipjack tuna.

Skipjack tuna larvae are widely distributed in the Pacific Ocean (Matsumoto, 1966; Ueyanagi, 1969). Ueyanagi (1969) reports that larvae were taken across the entire South Pacific between the equator and lat 10° S. Also, west of long 140° W larvae were taken as far south as lat 32° S. My study shows that the distribution of juvenile skipjack tuna is similar to the distribution of the larvae. In the North Pacific, skipjack tuna larvae have been found around Hawaii and across the entire Pacific between the equator and lat 20° N. In the western North Pacific, between long 160° W and the Asian continent, larvae have been taken almost as far north as lat 35° N (Ueyanagi, 1969).

My study indicates that gaps in the distribution of juvenile skipjack tuna in the Pacific reflect a lack of sampling. Higgins (1967) has a somewhat similar viewpoint. It is likely that the juveniles are as widely distributed as larval skipjack tuna in the North Pacific.

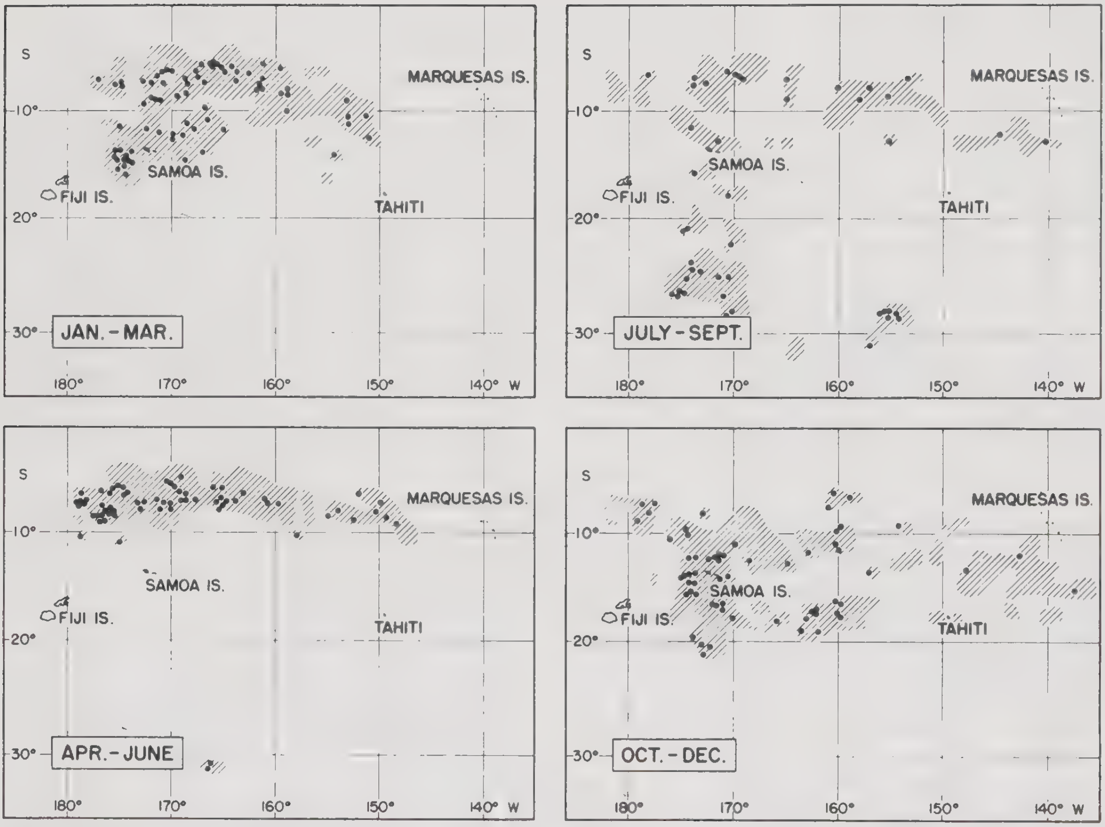
The distribution of juvenile skipjack tuna in the South Pacific by quarters of the year (all years combined) is shown in Figure 2. This is only the apparent distribution, however, because it reflects the operations of Samoa-based vessels. These vessels primarily seek albacore, and therefore they fish the areas where albacore catch rates tend to be high. In the first half of the year, vessels generally operate north of lat 20° S, and in June or July they move as far south as lat 30° S before heading north again (Otsu and Sumida, 1968). Samples were available mostly from north of lat 20° S, and juvenile skipjack tuna were found throughout the sampling range. In the third and fourth quarters, samples were available from a wider area, and again juvenile skipjack tuna were taken from almost the entire area sampled. Although seasonal coverage was incomplete throughout the total area, synoptic sampling would probably produce juveniles in all seasons and throughout the total area.

SEASONAL APPARENT ABUNDANCE

Hawaii

Apparent abundance is expressed here as number of skipjack tuna per 100 billfish stomachs. The apparent abundance of juveniles around Hawaii, all years combined, is shown in Figure 3. The juveniles were more numerous during July, August, and September. A peak in abundance usually occurred in August. These observations confirm Matsumoto's (1966) conclusion that skipjack tuna in the Hawaiian Islands spawned during the summer. He showed that the abundance of larval skipjack tuna peaked in July.

The apparent abundance of juveniles in 1963, 1964, and 1965 offers interesting contrasts. For example, in August 1963 the apparent abundance peaked sharply to 100 juveniles per 100 bill-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10°
SAMOA IS.
FIJI IS.
TAHITI
20°
30°
OCT. - DEC.
180°
170°
160°
150°
140° W

FIGURE 2.—Distribution of juvenile skipjack tuna (dots) by quarters of the year in the South Pacific. The shadings show the billfish sampling area.

fishes. Only small numbers were taken between January and June and between October and December. In 1964 and 1965 the summer peak in abundance was not so high; however, juveniles were more numerous in other months. The apparent abundance of juveniles was highest in 1964 when an average of 21.3 juveniles per 100 billfishes was taken. In 1965, an average of 19.1 juveniles was taken, and in 1963 the average was 12.4.

South Pacific

To examine the seasonal apparent abundance of juvenile skipjack tuna in the South Pacific, the area north of lat 10° S was considered separately from the area between lat 10° and 20° S (Figure 4). Because the coverage was poor in any one year, the data for all years were combined.

Juvenile skipjack tuna were taken throughout the year north of lat 10° S. Peaks in the apparent abundance were evident in April and October. Larvae have been taken throughout the year in the equatorial waters (lat 10° N to 10° S) of the central Pacific (Matsumoto, 1966). They were most numerous between April and July. Thus, the apparent abundance of the juveniles differs somewhat from that of the larvae in that a peak was absent in larval abundance in the latter half of the year. The difference in apparent abundance between the larvae and juveniles may not be real. The small number of stomachs collected in the latter half of the year may not have been adequate to reveal the true abundance of juveniles.

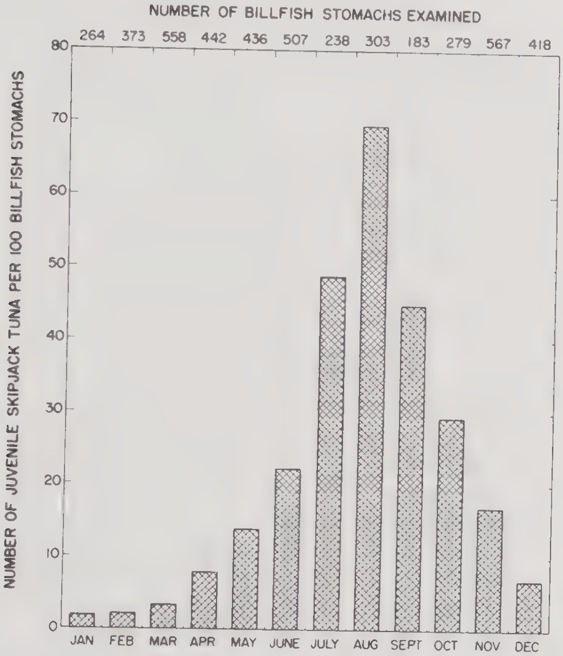

FIGURE 3.—Apparent abundance of juvenile skipjack tuna in Hawaiian waters, 1962-66.

Juveniles were taken in all months except July between lat 10° and 20° S. Here also the uneven sample sizes make the analysis of apparent abundance difficult. It appears, however, that juveniles were numerous from November to February. No comparable data on larval skipjack tuna in this area are available.

The apparent abundance of juvenile skipjack tuna was higher in 1964 than in 1965 in the South Pacific (Table 2). In 1964, juveniles were slightly more numerous north of lat 10° S than between lat 10° and 20° S. In 1965, however, juveniles were more numerous between lat 10° and 20° S than north of lat 10° S. Also they appeared to be more numerous in the South Pacific than near the Hawaiian Islands.

TABLE 2.—Annual apparent abundance of juvenile skipjack tuna in the central Pacific Ocean.

Year	Area	Number of billfishes	Number of juvenile skipjack tuna	Number of juveniles per 100 billfishes
1963	Hawaii	1,351	167	12.4
1964	Hawaii	1,608	342	21.3
	Equator-10° S	579	268	46.3
	10°-20° S	216	92	42.6
1965	Hawaii	1,008	193	19.1
	Equator-10° S	208	60	28.8
	10°-20° S	537	191	35.6

About 12% of the billfish stomachs from Hawaii contained one or more juvenile skipjack tuna, while 19% of the billfish stomachs from the South Pacific contained one or more juveniles. In both areas the largest number of juvenile skipjack tuna per stomach was 11; most of the stomachs from both areas had only one juvenile.

AGE AND GROWTH

The length-frequency distribution of juvenile skipjack tuna from Hawaii and the South Pacific is shown in Figure 5. Near Hawaii the smallest juvenile taken was 5.9 cm SL (standard

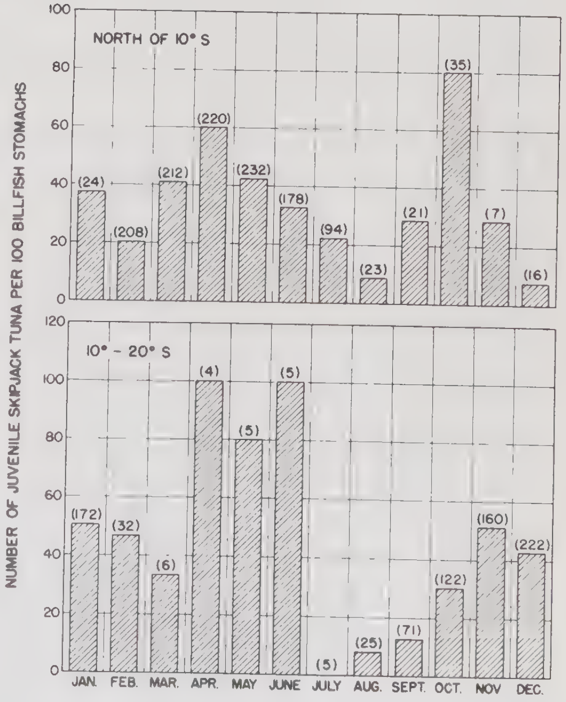

FIGURE 4.—Apparent abundance of juvenile skipjack tuna in the South Pacific. The figures in the parentheses are the number of billfish stomachs that were examined.

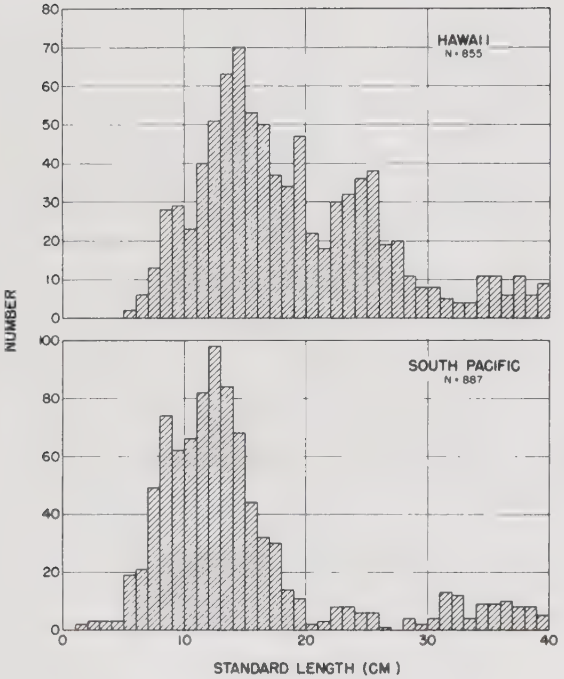

FIGURE 5.—Length-frequency distribution of juvenile skipjack tuna.

length). A prominent mode was located at the 14-14.9 cm size class, a lesser mode at 25-25.9 cm, and a relatively obscure mode was evident between 30 and 40 cm. The length frequencies of juvenile skipjack tuna from the South Pacific were similar to those from Hawaii. The smallest juvenile taken in the South Pacific was 1.6 cm SL. A prominent mode was evident at the 12-12.9 cm length class, a lesser mode between 20 and 30 cm, and a relatively obscure mode was apparent between 30 and 40 cm.

The monthly length-frequency distributions of the juveniles near Hawaii show well-defined modes in the summer and fall (Figure 6). Some of the length distributions have two or more well-defined modes. These modes probably represent progeny from two or more spawnings spaced more or less closely in time. An increase in size of the juveniles, as indicated by a progression of the modes, was evident in the monthly length distributions. In contrast, Higgins (1970) found that modal groups of juvenile skipjack tuna taken in midwater trawls did not show an increase in length with time.

Because the modal lengths increased with time, an attempt was made to describe the growth of the juveniles. To facilitate the designation of modes, the length data were smoothed by a moving average of three. Modes were not considered in samples that had fewer than 10 fish, nor in length groups containing fewer than 5 fish. The selected modes are given in Figure 7 and Table 3. Using the method of least squares, straight lines were fitted to groupings of modal points to represent the apparent growth of the juveniles. The slope of the lines for 1962, 1964-65, and 1965-66 indicates that juvenile skipjack tuna grow about 2.0 cm per month. The slope of the line for 1963-64 indicates a growth of 1.2 cm per month. These data suggest annual differences in the growth of the juveniles. I believe that an increment of 2 cm per month is the best estimate of the growth rate of juvenile skipjack tuna within the length range covered in this study. Rothschild (1967) used data from tag and recapture experiments and the von Bert-

TABLE 3.—Modes in the length-frequency distributions of juvenile skipjack tuna from Hawaii (from Figure 6).

Year	Month	Standard length (cm)		
1962	August	13.0	19.0	23.5
	September	20.0		
	October	27.0		
	November	22.0		
1963	June	13.5		
	July	13.5		
	August	9.5	15.5	
	September	15.5	22.0	
	November	23.5		
	December	24.0		
1964	April	30.0		
	May	19.0	25.0	
	June	15.5	25.5	
	July	8.5	13.5	
	August	11.0	18.5	
	September	12.5		
	October	14.5	23.5	
	November	23.5		
	December	25.0		
1965	April	35.5		
	May	12.5	26.5	
	June	9.5		
	July	15.5		
	August	10.5	14.5	18.5
	October	13.0	19.5	
	November	18.5		
1966	April	32.5		

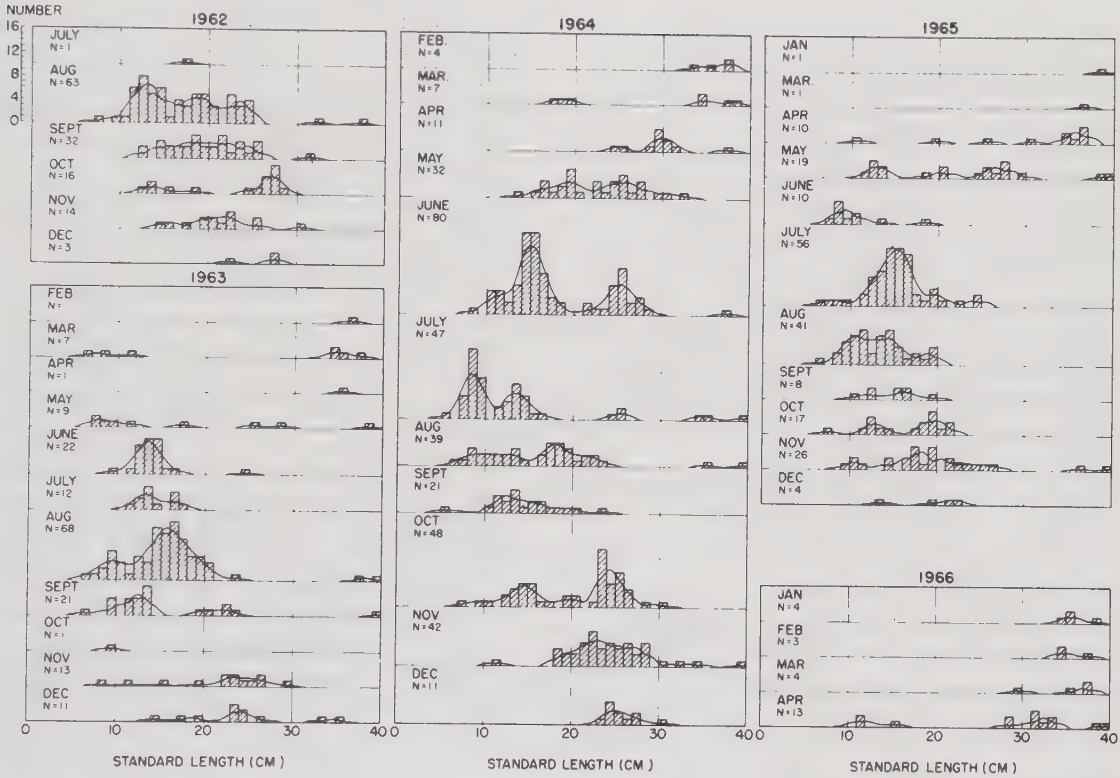

FIGURE 6.—Monthly length-frequency distribution of skipjack tuna from Hawaii.

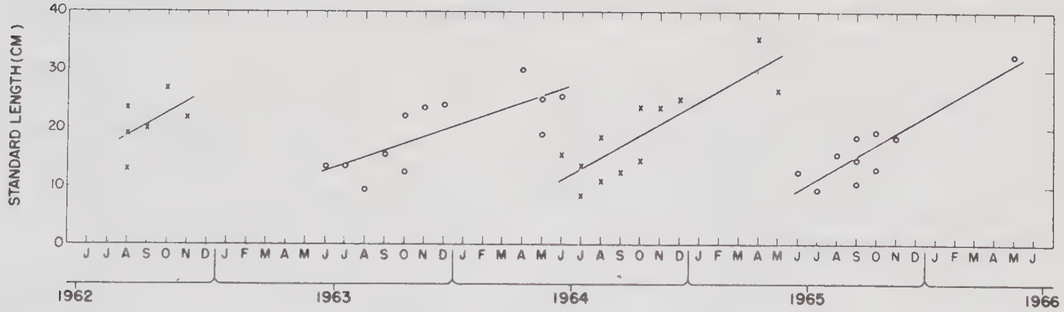

FIGURE 7.—Growth of juvenile skipjack tuna from Hawaii.

alanffy growth function to estimate skipjack tuna growth. He indicated that skipjack tuna between 44 and 72 cm grew about 16.6 cm per year or 1.4 cm per month. The deceleration in growth from 2.0 cm per month for skipjack tuna between 9 and 40 cm to 1.4 cm per month for fish between 44 and 72 cm is to be expected.

It is useful to determine the growth rate of skipjack tuna from hatching to 9 cm SL. These and other data may make it possible to estimate the age of skipjack tuna at various sizes. The growth rate of a related species, black skipjack, *Euthynnus lineatus,* between 17 and 75 mm SL has been determined (Clemens, 1956). In experiments conducted in shipboard aquaria Clemens showed that black skipjack grew 36.8 mm in 295 hr, which would be about 9 cm in a month. Houde and Richards (1969) reared larval little tunny, *E. alletteratus,* under laboratory conditions and reported similar growth rates. It was recently found that larval skipjack tuna have similar growth rates (personal communication, William J. Richards, Supervisory Zoologist, NMFS Tropical Atlantic Biological Laboratory, Miami, Fla. 33149, August 18, 1970). If larval skipjack tuna grow at the same rate (9 cm per month) for the first month and 2 cm per month for the next 11 months, then skipjack tuna 1 year old would be 31 cm SL.

Brock (1954) assumed that the modal sizes of fish between 40 and 50 cm FL (fork length) that appear in the Hawaiian skipjack tuna fishery during the summer represented 1-year-old fish. Forty to fifty centimeters for 1-year-old fish seems too high. Modal lengths typical of winter skipjack tuna in the Hawaiian fishery are 35, 50, and 70 cm FL (Rothschild, 1965). My data indicate that the 35-cm modal group that appears in the winter represents 1-year-old fish.

SPAWNING

In the Hawaiian area, juvenile skipjack tuna smaller than 10 cm were found during 7 months in 1963 and during 5 months in 1964 and 1965 (Figure 6). This suggests a protracted spawning season and nearly continuous recruitment of juveniles. The catch of larvae indicates that spawning begins in March, peaks in July, and declines sharply in September and October (Matsumoto, 1966).

The Hawaiian skipjack tuna fishery peaks in the summer when the bulk of the catch is composed of "season-size" fish larger than 60 cm (Rothschild, 1965). Larval and juvenile skipjack tuna also are most numerous during the summer, which suggests that the large fish spawn in Hawaiian waters. The presence of juveniles in the spring and fall, although in lesser numbers, indicates that spawning also takes place then. Rothschild (1965) has hypothesized that at least one subpopulation spawns in Hawaiian waters. The protracted spawning season may indicate that more than one subpopulation spawns here.

In the South Pacific between lat 5° and 20° S, the spawning season is more protracted than in Hawaiian waters. Juveniles smaller than 10 cm SL were taken in almost every month north of lat 10° S. Between lat 10° and 20° S they were taken in all months except March, April, June, and July (Figure 8); the reason for their absence in these months may be inadequacy of sampling. The area south of lat 20° S was somewhat different. Although sampling was sparse, the length-frequency distribution consistently showed few small juveniles, which indicates little or no spawning in this area.

The length-frequency distribution of juvenile skipjack tuna north of lat 10° S and between lat 10° and 20° S indicated a progression of modes (Figure 8). However, a plot of the modal lengths indicated no growth. The cause of this may be a protracted spawning season and inadequacy of samples. Also juveniles appear to migrate southward as they grow. Only small numbers of juveniles larger than 20 cm SL were taken north of lat 20° S, and most of the juveniles taken south of lat 20° S were larger than 20 cm SL.

ACKNOWLEDGMENTS

Thanks are due the research assistants at the NMFS Hawaii Area Fishery Research Center who examined the billfish stomach contents for juvenile skipjack tuna and aided in summarizing part of the data. The portion of the study in the South Pacific would not have been possible without the cooperation of the crews of the many fishing vessels from Japan and the Republic of Korea. I thank William J. Richards, NMFS, Miami, Fla.; Walter T. Pereyra, NMFS, Seattle, Wash.; and Witold L. Klawe, Inter-American Tropical Tuna Commission, La Jolla, Calif. for reviewing the manuscript.

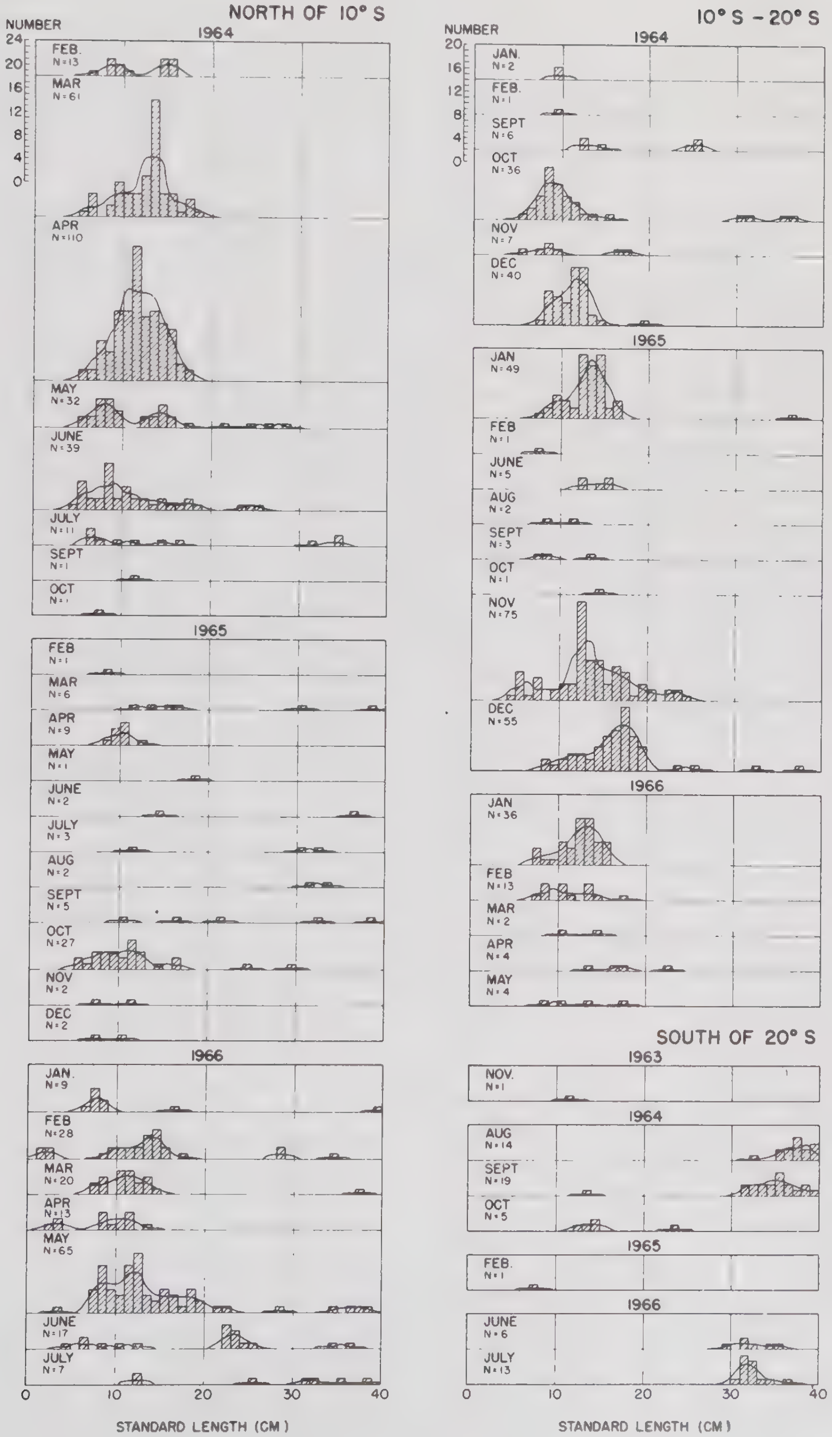

FIGURE 8.—Monthly length-frequency distribution of juvenile skipjack tuna north of lat 10° S, lat 10°-20° S, and south of lat 20° S in the South Pacific.

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Behavior of Skipjack Tuna, *Katsuwonus pelamis*, as Determined by Tracking with Ultrasonic Devices

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YUEN, H. S. H. 1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Bd. Canada 27: 2071–2079.

A 50-kHz transmitter was placed in the stomach of a 44-cm (estimated) skipjack tuna, *Katsuwonus pelamis*, at Kaula Bank, Hawaii. With a few interruptions the fish was tracked from August 30 to September 6, 1969. The fish made nightly journeys of 25–106 km away from the bank and, with one exception, returned to the bank every morning to remain there for the day. Another skipjack tuna, about 40 cm long, was tracked for 12 hr at Penguin Bank, Hawaii. It also stayed at the bank during the day and left at night. Both fish swam close to the surface at night but swam at various depths during the day. The repeated morning returns of the skipjack tuna to Kaula Bank imply that skipjack tuna can navigate and that they have a sense of time.

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THE FOREMOST POSITION of the fishery for skipjack tuna, *Katsuwonus pelamis*, in Hawaii is largely maintained by an annual influx of "season" fish of 60–70 cm length (Uchida, 1967). As important as this migratory component is to the fishery, its movements into, within, and out of the Hawaiian area remain a mystery. Shippen (1961), after an analysis of the distribution of skipjack tuna catches in time and space, suggested that the fish entered the fishery from the west and departed towards the west. On the other hand, a method for predicting the annual catch of skipjack tuna of the Hawaiian fishery can be explained only by hypothesizing entry from the northeast (E. C. Jones, personal communication). The capture in Hawaii of two skipjack tuna tagged off Baja California (Rothschild, 1965) gave some support to this hypothesis. A study of movements within the fishery (Royce and Otsu, 1955) through the analysis of data on sightings and visual tracking of surface schools was inconclusive because of the effects of weather conditions on sightings and the brevity of tracking attempts, which did not exceed 15 min.

Smaller skipjack tuna about 40–50 cm long, although they too are seasonal, are caught in small quantities throughout the year. Recoveries of tagged skipjack tuna of this size revealed only localized movements with no obvious pattern (Yamashita and Waldron, 1959). An association of these fish with banks is indicated by the common practice of fishermen to go to areas with banks to fish them. The relation between fish and bank is unknown.

The increasing success at tracking fish bearing ultrasonic transmitters (Trefethen, 1956; Trefethen et al., 1957; Johnson, 1960; Novotny and Esterberg, 1962; Bass and Rascovich, 1965; Hasler et al., 1969; Henderson et al., 1966;

Printed in Canada (J1820)

Dizon et al., 1970) offered an approach for studying the movements of the skipjack tuna. In August 1969, the BCF (Bureau of Commercial Fisheries) Biological Laboratory, Honolulu (now the National Marine Fisheries Service), initiated field work to determine the feasibility of tracking the large commercially important skipjack tuna equipped with ultrasonic transmitters for extended periods and to obtain information on the behavior of the smaller skipjack tuna associated with banks.

As large skipjack tuna were not available at the time, work was limited to smaller fish. From August 30 to September 9, 1969, ultrasonic transmitters were placed in two skipjack tuna and tracked. Methods and results are described and discussed in this report.

MATERIALS AND METHODS

Transmitter characteristics are listed below. The transmitters contained a magnetic reed switch and were activated by the removal of a magnet taped on the outside (Fig. 1).

FIG. 1. Tag and applicator.

Frequency	50 ± 1 kHz	Shape	Cylindrical capsule with rounded ends
Repetition rate	2 pulses per sec		
Pulse length	50 msec	Dimensions	8.1 cm long, 2.0 cm diam
Power output	52 db relative to 1 microbar at 1 yard	Weight in air	62 g
		Lifespan	250 hr

Prior to the field work, trial runs were made on captive fish to test a tagging technique and to determine the effects of the transmitter on skipjack tuna. The trials were made on two skipjack tuna 48 cm long. These fish were part of a school that was held in a plastic swimming pool with a capacity of 45 m^3. The transmitters were placed in the stomachs of the fish. The two skipjack tagged in this manner behaved as the other members of the school held in captivity and were not distinguishable from them. Both tuna, one dissected 3 days and the other 4 days after the insertion of the transmitters, contained the remains of food fish in their stomachs, indicating that they had resumed feeding.

Skipjack tuna to be tracked were caught by trolling lures with barbless hooks. As soon as a lure was struck the ship was reversed and the line pulled in by hand evenly and firmly. When the fish was alongside the ship it was scooped up in a dipnet. The hook was removed and the fish tagged while still in the net. Tagging consisted of inserting the transmitter into the pharynx with a plastic applicator (Fig. 1) and allowing the fish to swallow the transmitter. The fish was released by lowering the net into the water.

Neither of the two fish tracked was measured. The length of the first fish was estimated by taking the mean length of 11 fish that were caught from the same school. The size of the second skipjack tuna was gauged by eye.

Signals from a tag were received through the listening mode of the continuous-transmission, frequency-modulated sonar (Yuen, 1968) on the research vessel *Townsend Cromwell*. The hydrophone, located 4 m below the surface, had a beamwidth (at the down 6 db level) of 6° horizontally and 15° vertically. The tag could be detected as far as 2.3 km with this equipment.

During tracking operations, contact with the transmitter was maintained by continually scanning in bearing and tilt about 6° on either side of the last observed position. The ship was maneuvered to maintain a distance of approximately 1 km from the tagged fish to avoid affecting the behavior of the fish. Because of errors in estimating the distance of the transmitter by its signal strength and confusion in operations, however, there were a few occasions when the distance between ship and transmitter was as little as 200 m or was greater than 2.3 km, the detectable range.

During tracking the following data were recorded: time of day, transducer bearing, transducer tilt, ship's course, ship's speed, receiver gain setting, and signal strength. Also recorded were all orders directing the ship's movements and the time the orders were given. Ship's course was read to the closest degree from a repeater of the ship's gyrocompass. Speed was measured to tenths of knots by an electromagnetic underwater log. Signal strength was measured by an oscilloscope. These data were scheduled to be taken at 5-min intervals. In practice the recording interval ranged from 2 to 10 min, but most were at 5 min. The officer on watch was asked to plot the ship's position every hour but he often did so more frequently. Positions were determined by radar at Kaula Bank and by loran A at Penguin Bank (Fig. 2).

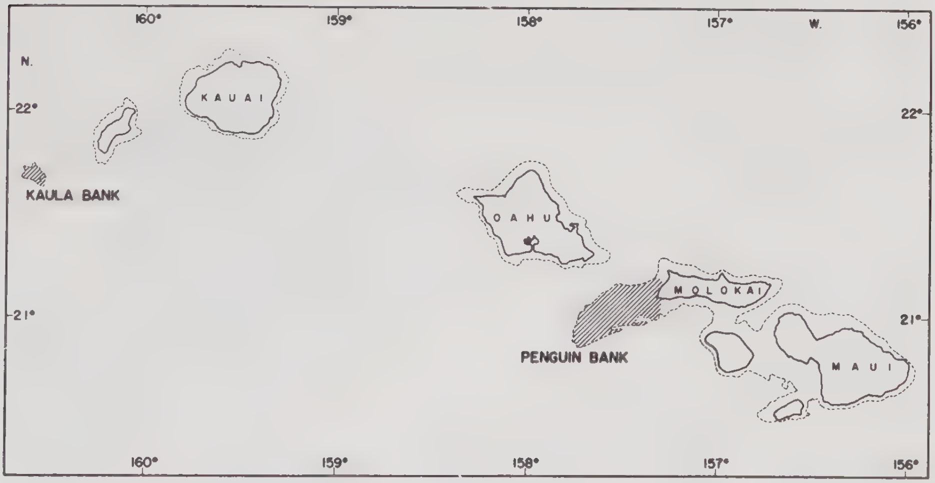
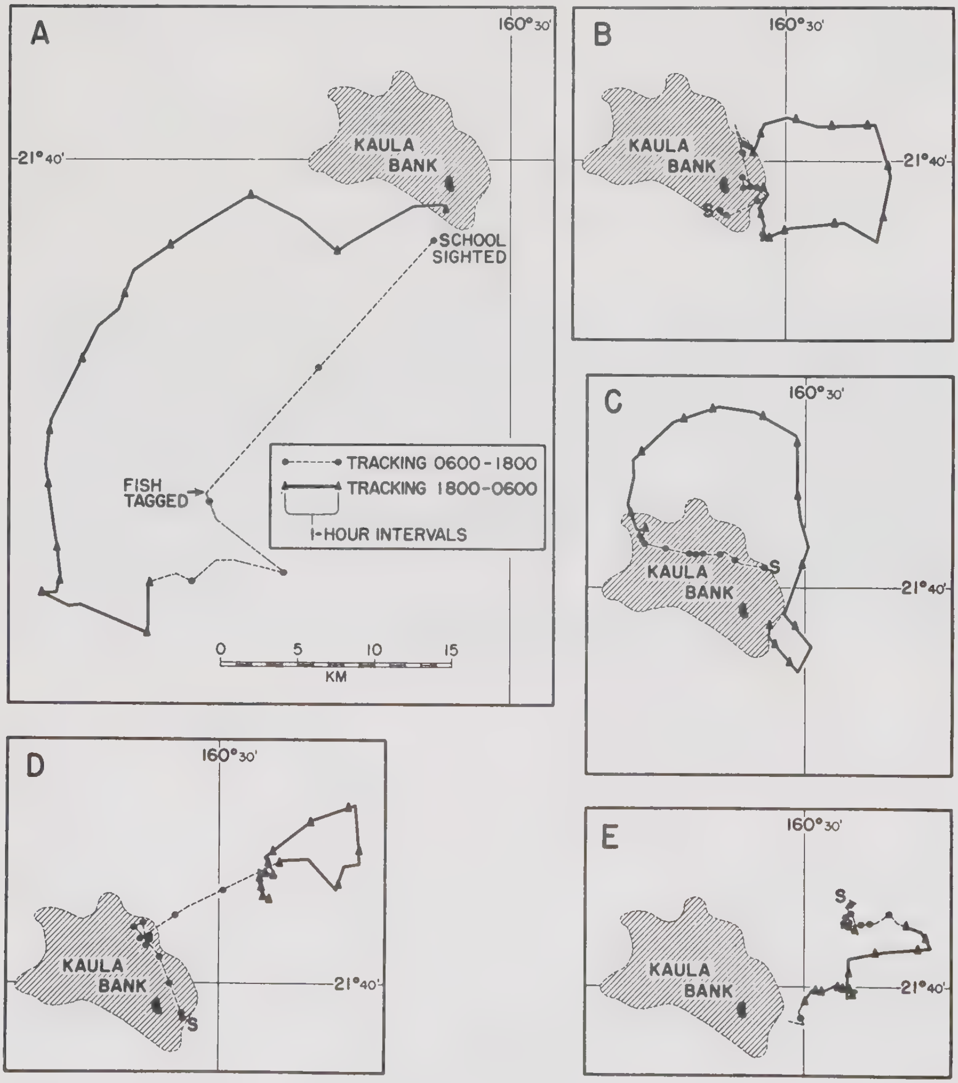


FIG. 2. Location of Kaula Bank and Penguin Bank.

Because the fish were likely to be within 1 km of the ship and certainly not farther than 2.3 km and because the navigational error term did not justify further refinement, the positions of the fish were considered to be the same as the ship's when the data were analyzed.

RESULTS AND DISCUSSION

The first skipjack tuna was tagged and released at 2:52 PM on August 30. It was estimated to be 44 cm long. It was in a school that had been sighted at 1:05 PM at Kaula Bank and had been pursued for 28 km (Fig. 3) before the fish was tagged. The marked fish was under continuous surveillance until 8:00 AM, August 31, when contact was lost. It was found at 9:32 AM, August 31 and tracked continuously until 10:31 AM, September 1, when the sonar broke down. A trip was made to Honolulu to repair the sonar, and the ship was back at Kaula Bank at 6:30 AM, September 3, at which time search for the signal


A
160°30'
21°40'
KAULA BANK
SCHOOL SIGHTED
FISH TAGGED
TRACKING 0600-1800
TRACKING 1800-0600
1-HOUR INTERVALS
0 5 10 15
KM
B
160°30'
KAULA BANK
21°40'
S
C
160°30'
KAULA BANK
S
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D
160°30'
KAULA BANK
21°40'
S
E
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S
KAULA BANK
21°40'

FIG. 3. Track of tagged skipjack tuna at Kaula Bank: (A) from 2:52 PM, August 30, to 6:00 AM, August 31; (B) from 6:00 AM, August 31, to 6:00 AM, September 1; (C) from 7:38 AM, September 3, to 6:00 AM, September 4; (D) from 6:00 AM, September 4, to 6:00 AM, September 5; (E) from 6:00 AM, September 5, to 7:30 AM, September 6.

from the skipjack tuna was started. At 7:38 AM contact with the transmitter was resumed. On September 4 the fish was lost from 3:45 AM to 5:42 AM. From 6:38 AM to 9:12 AM that same morning acoustic contact was broken because the fish was too close to shore for the ship to follow. It was tracked nonetheless because the school it was in was visible. Contact with the fish was lost twice more: 4:30–4:55 AM on September 5 and 1:57–3:02 AM on September 6. Tracking was voluntarily ended at 7:30 AM, September 6.

We terminated tracking the skipjack tuna at Kaula Bank to collect comparative data from another bank. At 12:55 PM on September 8 a second skipjack tuna about 40 cm long was tagged at Penguin Bank. This fish was tracked until 12:45 AM, September 9, at which time it was lost.

The fish at Kaula Bank exhibited a pattern. At about nightfall each day, the fish left the bank to follow an irregular and wide-ranging path offshore during the hours of darkness; by about sunrise it was back at the bank and it remained there until night (Fig. 3). Even though the route differed from night to night the fish was back at the bank five of the six mornings it was observed. On the excepted morning it was 9 km from the bank and it remained there throughout the day. It was at the bank the following morning after a night of traveling. The fish at Penguin Bank also left the bank at the end of the day (Fig. 4).

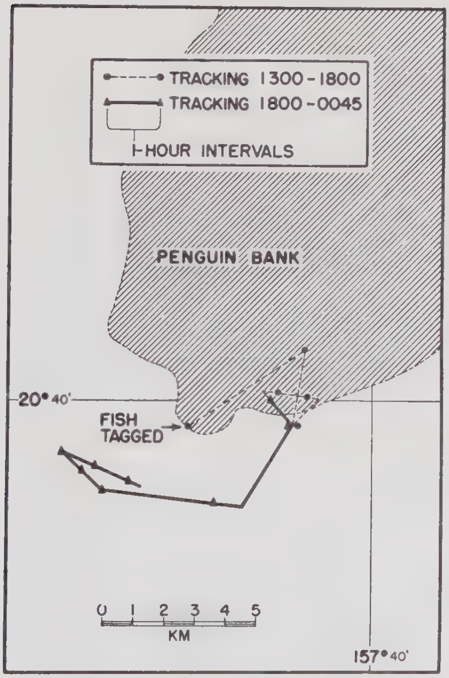

FIG. 4. Track of tagged skipjack tuna at Penguin Bank.

On its nocturnal journey the fish at Kaula Bank covered distances of 106, 31, 40, 36, and 25 km, in that order. The first night's journey was considerably longer than the others. The long pursuit before tagging is suspected as a cause of the atypical length of that run.

During the day a school of skipjack tuna was often visible at the position whence the transmitter signals were being received. On several occasions, during both day and night, the ship inadvertently approached within 200 m of the tagged fish. When the sonar was switched to the active mode at these times, many targets were observed in the vicinity of the tag. I assumed from these observations that the tagged skipjack tuna rejoined their schools and that their behavior was typical and representative of other skipjack tuna.

To investigate in more detail the daily periodicity evident from the fish's track, the means and variances of the distance traveled for each hour of the day were calculated. The variances (Fig. 5A) fell into three levels: less than 1.1, 2.0–7.5, and greater than 9.5. At the highest level the primary source of variation was the unusual distance traveled during the first 15-hr period after tagging. The means and variances were then recalculated without these extra high values (Fig. 5B and C).

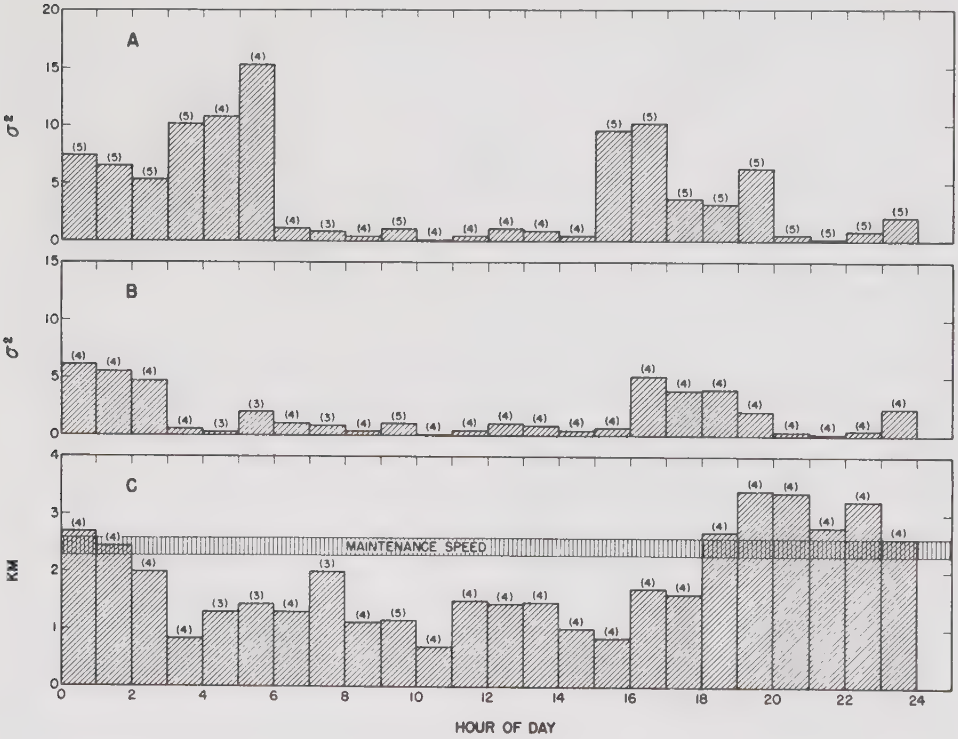

FIG. 5. Daily swimming pattern: (A) variance of distance traveled per hour calculated from all data; (B) variance of distance traveled per hour excluding data of first 15 hr; (C) mean distance traveled per hour.

The prominent feature of the histogram of distance traveled per hour (Fig. 5C) is the higher level from 6:00 PM to 2:00 AM. The increase, occurring as it did at 6:00 PM, immediately suggested that it was triggered by sunset, which occurred between 6:09 and 6:17 PM on the days concerned. The data from individual days, however, show that the start of the increase occurred between 4:00 and 7:00 PM. This 3-hr spread is reflected in the higher level of variances during that period (Fig. 5B). Another period of higher variances from 12:00 AM to 3:00 AM is obvious in Fig. 5B. This is the period during which the changeover from the high rate of travel to the lower rate began.

The distances traveled were based on positions of the ship so that they indicate the net hourly movements of the ship and not necessarily those of the tagged fish. Under the conditions of collection of the data, the distance traveled by the ship will always be less than that traveled by the fish but will approach that of the fish as the route of the fish approaches a straight line. The distance traveled by the ship could be zero if the fish made many turns. Depending on the circumstances, then, changes in the distance traveled (Fig. 5C) could mean changes in swimming speed, changes in swimming pattern, or both.

For hydrodynamic and physiological reasons tunas swim continuously. The swimming occurs at various minimum speeds. The minimum speed for skipjack tuna is not known but it has been calculated for *Euthynnus affinis*, a closely related species (Magnuson, 1970). For an *E. affinis* of 44 cm fork length minimum speed is 2.3–2.6 km/hr. If we assume that the tagged tuna did maintain this speed, then from 2:00 AM to 6:00 PM, when the rate of travel was below this level, its swimming pattern must have included much turning.

When the hydrophone is at 0° (aimed horizontally) to 7½° vertical tilt to receive the signal, the fish may be at any depth from the surface to about 500 m. If the signal is received at a tilt greater than 7½°, however, the fish cannot be within 4 m of the surface. The percentage of tilt angle records that exceeded 7½° was calculated for every hour of the day (Fig. 6). Since the intervals between readings were fairly constant, this percentage also represents the percentage of time that the fish was away from the surface for certain. From 5:00 AM to 8:00 PM the fish at Kaula Bank (Fig. 6A) spent an average of 29% of the time away from the surface. For the remaining hours the average was 2.6%. This average should be less because the readings greater than 7½° between midnight and 2:00 AM were obtained one night when the ship inadvertently passed directly over the fish. From the time it was tagged until 5:00 PM the fish at Penguin Bank spent a large proportion of its time away from the surface (Fig. 6B). Beyond 5:00 PM until it was lost, however, the hydrophone was aimed horizontally 92% of the time and was tilted a maximum of 5° the rest of the time.

The following picture of the behavior of skipjack tuna that are associated with banks can be drawn from these results. They have a general daily pattern. They usually spend the day at the bank, where they swim to and fro and are away from the surface a good part of the time. This type of swimming is probably associated with searching for food and feeding. Later in the day, within a couple of hours of sunset, they leave the bank and swim with few changes in direction until approximately 2:00 AM, when they seem to adopt a more erratic swimming pattern. Although they leave the bank by different routes

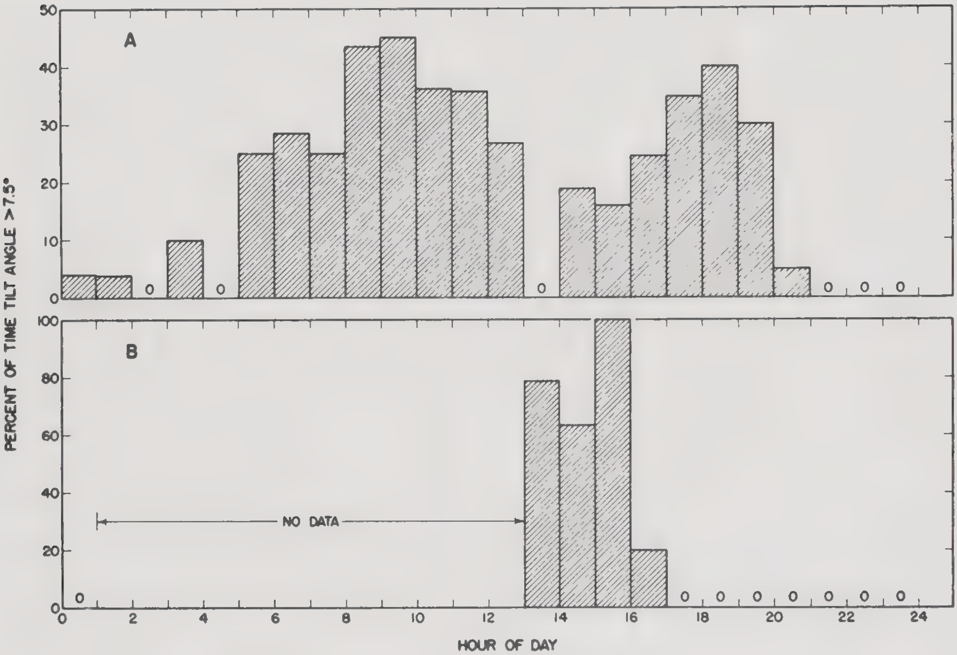

FIG. 6. Daily pattern of swimming depth: (A) skipjack tuna tagged at Kaula Bank; (B) skipjack tuna tagged at Penguin Bank.

from day to day, they are usually back at the bank by sunrise. They are presumed to be close to the surface throughout the night.

The repeated returns to the same spot by the fish at Kaula Bank after journeys of 25–106 km by various routes imply that skipjack tuna can navigate. Their consistent arrival times suggest that they have a sense of time. It is interesting to note that from 3:00 AM to 6:00 AM of the first morning after it was tagged, when it was unusually far from the bank, the tuna at Kaula Bank averaged 8 km/hr, seven times its average speed for that time of the day, as if it were compelled to arrive at the bank by a certain time.

On November 30, 1969, a skipjack tuna (52.2 cm fork length) marked with a Floy dart tag was caught at Kaula Bank (R. N. Uchida, personal communication). It was tagged on May 19, 1969, at 22°01′N and 155°55′W, a position 519 km from Kaula Bank. This recovery and the fact that skipjack tuna over 60 cm long seldom occur at banks indicate that they are not lifetime residents of a bank but come for an undetermined duration and leave.

Skipjack tuna over 60 cm long have different food preferences from those less than 50 cm long (Yuen, 1959). The swimming behavior of the fish tracked at Kaula Bank and Penguin Bank was typical of foraging tuna. This evidence suggests that food preferred by the small but not by the large tuna is found at the banks and that the small tuna frequent the banks for the purpose of feeding.

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7157

An Evaluation of a Continuous-Transmission, Frequency-Modulated Sonar in Fishery Research

Une evaluation du sonar a transmission continue et frequence modulee (CTFM) pour la recherche halieutique

Un sonar à transmission continue et fréquence modulée (CTFM) à été utilisé dans des études effectuées sur le listao (*Katsuwonus pelamis*) par le Laboratoire de biologie du Bureau des pêches commerciales des Etats-Unis à Honolulu, depuis 1966. Les capacités du sonar CTFM sont précisées, en ce qui concerne la portée, la définition et la vitesse d'information. On a attribué l'aisance avec laquelle les cibles sont détectées à sa transmission continue et à sa vitesse d'information élevée. A son début, l'emploi du sonar CTFM a entraîné des problèmes (1) de retards dans la réparation et le réglage provenant d'un personnel inexpérimenté et d'un manque de pièces, et (2) de conversion analogique-digitale de données enregistrées à un rythme très rapide. Le sonar CTFM a été utilisé pour rechercher et suivre le listao. Pendant les opérations de poursuite, des difficultés ont été provoquées par des déplacements brusques et imprévisibles, une faible propriété réfléchissante du son et une tendance de ces poissons à faire des émulsions d'air dans l'eau en surface. Un petit émetteur placé dans un poisson a permis de réussir des opérations de poursuite. Les problèmes englobant les rythmes de détection et l'identification de l'écho pendant les opérations de recherche sont discutés. On résume les informations obtenues sur le comportement du listao grâce à l'emploi du sonar. L'utilisation des sonars CTFM dans l'industrie des pêches est discutée.

Evaluación del sonar de CTFM en la investigación pesquera

En el Laboratorio de Biología que la Oficina de Pesca Comercial de los E.U.A. tiene en Honolulú, se emplea desde 1966 un sonar de transmisión continua y frecuencia modulada (CTFM) en el estudio del listado, *Katsuwonus pelamis*. Se decriben las posibilidades de este aparato en lo relativo al alcance, resolución y velocidad a que suministra la información. La facilidad con que se localizaron los objectivos se atribuyó a su transmisión continua y a la gran rapides con que facilita los datos. Los problemas relacionados con el uso inicial del sonar CTFM fueron: (1) retrasos en las reparaciones y ajustes debidos a la inexperencia del personal y a no disponerse de piezas y (2) convertir a gran velocidad los datos registrados de digital a análogos. El sonar de CTFM se empleó para buscar y seguir el listado. Durante la persecución crearon dificultades sus movimientos repentinos e imprevisibles, lo mal que reflejan los sonidos y su tendencia a crear burbujas de aire mientras están en la superficie. Dio buenos resultados un pequeño transmisor ultrasónico que se había puesto en los ejemplares que se iban a seguir. Se examinan los problemas que plantea la velocidad de localización e identificación de los objetivos durante la búsqueda. Se presenta resumida la información sobre el comportamiento del listado obtenida empleando el sonar. Se discute el empleo de sonar CTFM por la industria pesquera.

IN the last decade two interesting developments in underwater acoustic equipment have been applied towards fishery problems. Both of these, the sector-scanning sonar and the continuous-transmission, frequency-modulated (CTFM) sonar, represent departures from conventional pulsed sound techniques to provide high resolution and high rates of information. Although they are quite different from each other, both use narrow beams and rapid scanning to accomplish their objectives. The sector-scanning sonar scans bearing as its first order of scanning while the CTFM sonar scans range as its first order of scanning. Their potential as demonstrated by initial trials and applications in fishery research (Harden Jones and McCartney, 1962; Tucker and Welsby, 1964; Cushing and Harden Jones, 1966; Hester, 1967; and Yuen, 1968) has attracted considerable interest.

A CTFM sonar was purchased by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, in 1966 to further its studies on tuna behaviour and distribution. The CTFM sonar was chosen over conventional sonars because we believed that the conventional sonars would be inadequate for keeping in contact with the quick moving tunas. The project involving the CTFM sonar set out to do the following: describe the short-term movements, both horizontal and vertical, of the skipjack tuna, *Katsuwonus pelamis*, and investigate the relation between the movements and environmental features; measure such schooling parameters as school size, density, configuration, and stability; describe the migration route of skipjack tuna; and evaluate the effectiveness of the CTFM sonar in locating subsurface tunas.

This evaluation of the CTFM sonar is based on my working experience with it since 1966 and is presented largely from a non-technical viewpoint. The report includes the capabilities and limitations of the CTFM sonar, problems encountered in its use, corrective measures, results of current work and a discussion of its potential use in the fishing industry.

CAPABILITIES AND LIMITATIONS

The distance an object can be detected by sonar depends on how well the object reflects the sonar signals. The CTFM sonar has a range of 1600 m for objects with echoes of sufficient strength. The detection ranges of various species (Table I) are reproduced from Yuen, 1967.

TABLE I. MAXIMUM RANGES AT WHICH VARIOUS ANIMAL TARGETS WERE OBSERVED ON THE CRT DISPLAY

Mode	*Target*	*Maximum range (m)*
Search	Dead skipjack tuna (65 to 75 cm fork length)	
	One	235
	Two (one above other, 30 cm apart)	340
	Three (one above other, 35 cm apart)	380
	Surface skipjack tuna schools (1 to 11 kg)[1]	650
	School of yellowfin tuna (*Thunnus albacares*) (18 kg)[1]	545
	Subsurface fish (unidentified)	389
	Whitetip shark (*Carcharhinus longimanus*)[1]	340
	Billfish (Istiophoridae)[1]	280
	Porpoise[2] (probably *Stenella attenuata* or *Steno bredanensis*)	
	One	ca. 400
	Group	800
Classify	Dead skipjack tuna (65 to 75 cm fork length)	
	One	130
	Two (one above other, 30 cm apart)	130
	Three (one above other, 35 cm apart)	130

[1] Identified visually at the sea surface.

[2] Identified from the display of their own sounds on the CRT.

Although skipjack tuna were detected up to 650 m, the limit of detection for this species was usually 300 to 400 m.

The CTFM sonar has a high resolution mode called the classify mode. In this mode the sonar has a range resolution of 0.0019 times the target distance and a bearing resolution of 0.01 times the target distance. This means that if there are two targets one behind the other relative to the sonar transducer at a distance of 100 m, they would need to be at least 19 cm apart to be recognizable as two targets. If the two fish were at different bearings but at the same range they would need to be 1 m apart at a distance of 100 m to be distinguishable as two targets.

The sonar can be operated at a ship's speed of 18 km/h (10 kn). Beyond 11 km/h (6 kn), however, noise level begins to interfere with effective operations. At 15 km/h (8 kn) virtually no useful information can be obtained.

The outstanding feature of the CTFM sonar is its continuous transmission of acoustic energy. As illustrated in fig 1, the projected signal is frequency modulated in a sawtooth pattern. Subtracting the frequency of the outgoing signal from that of the echo results in a difference frequency labelled *df* in fig 1. The magnitude of the difference frequency is proportional to the time lapse between the transmission and the return of the echo. The time lapse, labelled *a* in fig 1, is in turn proportional to the distance of the reflecting object so that the difference frequency is also proportional to this distance. Information on the target is received throughout the sawtooth period after the time lapse *a*. In a conventional pulsed sonar the information is only available for the length of the pulse.

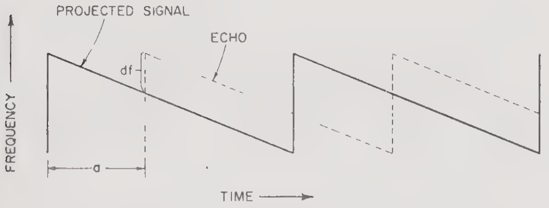

Fig 1. Pattern of frequency modulated signal and echo. a = loss time, df = difference frequency

Since no information is received during the time lapse *a*, this period is called the *loss time*. There is a method to recover the information during the loss time but it is not incorporated in our sonar.

Loss time increases as target distance increases so that the length of time that information is received varies inversely with target distance. Information time can be lengthened proportionately by lengthening the period of the sawtooth. The gain in information time by this method, however, is made at the expense of range resolution.

The difference frequency is processed through a frequency analyzer of 100 bandpass filters. The outputs of the filters are read sequentially every 7 msec. The 7 msec. can be divided into a reading time of 5 msec. and a pause of 2 msec. A high information rate is the result of this rapid reading rate.

How do the attributes of continuous transmission and high information rate contribute to the performance of the sonar in locating a target? The question can best be answered by reviewing an experiment. A target was placed in the water. Its depth was changed at various times from 10 m to 80 m below the surface. The ship repeatedly went past the target at various distances at a speed of 7.5 km/h (4 kn). The sonar operators were instructed to find the target with no prior knowledge about its position. Furthermore, the operations of the sonar was restricted to a standard scanning pattern for searching. The target was detected 23 out of the 24 times the ship passed within sonar range of the target. In my opinion, the high detection rate was possible only because of the features of rapid information and continuous transmission of the sonar.

The high certainty of detecting objects has provided an unexpected benefit. The sonar has been used successfully in locating submerged instruments which had lost their surface markers.

PROBLEMS

Some problems were encountered in the use of the CTFM sonar. Some were solved; others corrected themselves with time; others still remain. Corrective measures taken are described.

One early problem was the time spent on repairs and adjustments. Because the equipment was new, maintenance personnel were unfamiliar with it. As a result repairs and adjustments, even minor ones, required much time. As personnel gained experience, the seriousness of the problem diminished.

The sonar has many specialized components whose replacements are difficult to obtain. Some parts are not available in Hawaii. Others are constructed as they are ordered; these are not readily available anywhere. Delays of various durations have resulted when parts were not on hand. In the most extreme case a high precision potentiometer required 18 months to obtain. During that time the classify mode was out of order. Delays in repairs have been considerably reduced but not entirely eliminated by storing an extensive supply of spare parts, particularly critical ones.

The data collected during sonar operations were recorded on a 14-channel, analog, magnetic tape recorder. To make the data acceptable for processing by a computer, conversion from analog to digital was necessary. A problem was encountered in digitizing of the sets of the 100 sequential readings of the frequency analyzer. It was necessary to signal the analog-to-digital converter to start precisely at the beginning of each set. Failure to do so would have caused the sets to become mixed, which would have rendered the data meaningless. Efforts at instructing the computer directing the conversions to detect the exact starting time and then to signal the converter failed because there was insufficient time between the detection process and the signalling process. Conversions were successfully made when an electronic device was added to the system to suppress signals activating the converter unless they began at the same time as the sets of reading from the frequency analyzer.

The operations of the CTFM sonar were of two types. It was used primarily to track skipjack tuna which had been located and identified visually. Tracking operations were for the purpose of obtaining behaviour observations. The sonar was used secondarily to find subsurface schools of skipjack tuna. Searching and tracking operations were both hampered by the limited range at which skipjack could be detected. Within the area of the Hawaiian skipjack tuna fishery, where most of the work with the sonar has been done, surface schools of this species have been sighted at a rate of approximately one per 300 km². Even if one supposes that for every school at the surface there is another beneath the surface, a sonar scanning a radius of 400 m on a ship travelling at 10 km/h would have an expected detection rate of one school per 10 hours. This result is based on the assumption that the skipjack schools move randomly at a speed of 5 km/h.

The effective range of 300 to 400 m for skipjack tuna was found to be inadequate during tracking operations. The fish with their sudden and unpredictable movements moved out of range before the ship could be manoeuvred in response.

A difficult problem in searching with a sonar is target identification. At present the more experienced sonar operators believe that they can identify echoes of skipjack tuna and sharks. The identification criteria, however, are subjective and therefore difficult to describe. An attempt is being made to formulate objective criteria of identification. To do this, sonar records of positively identified species will be processed through a computer for analyses of strength, movement, and spacing of echoes with respect to time. Since the information from the sonar has been recorded in cycles of 7 msec. very detailed analyses will result in a practical method of identifying species.

Skipjack tuna at the surface presented special problems which made tracking them difficult. The strength of echoes of skipjack tuna, as with most fishes, depends upon the orientation of the fish to the sonar. Echoes are strongest with a lateral aspect of the fish and weakest with the head and tail aspects. Dorsal and ventral aspects result in echoes which are almost as strong as those from a lateral aspect. Echoes from fish below the sonar, therefore, are consistently fairly strong because the fish present a dorsal aspect regardless of the direction they are swimming. Echoes from surface fish, on the other hand, vary widely in strength as the fish change their directions. Furthermore, when one is tracking a fish one is likely, most of the time, to be behind the fish, where the echoes are the weakest.

Another problem with skipjack tuna at the surface is that they have a tendency to break through the surface and thus introduce masses of air bubbles into the water. Unwary sonar operators have often concentrated on the echoes from these air bubbles while the fish moved away. A tracking technique with some degree of success was to have the operator constantly scan below the fish in order to detect them when they left the surface. Of course, the procedure did not work if the fish moved out of range before leaving the surface.

In the summer of 1969 a major advance in tracking was made. A skipjack tuna that had been induced to swallow a small 50 kHz transmitter was followed with the sonar for six days; another for 12 hours. The transmitters could be detected up to 2.5 km. The transmitters which were used had a life of 10 days but transmitters lasting 60 days are now available.

RESULTS AND COMMENTS

The CTFM sonar has been used by the Biological Laboratory, Honolulu, primarily as a tracking device to study the behaviour of skipjack tuna. Results thus far indicate that: (1) skipjack tuna will go as deep as 200 m; (2) larger skipjack tuna tend to go deeper than smaller ones; (3) small skipjack tuna remain close to the surface at night but make many excursions away from the surface during the day; (4) the speeds of their vertical movements average 0.3 m/s and can be as high as 3.3 m/s.

Behaviour information of the type mentioned is useful in the design of fishing gear and strategy and thus contributes to the fishing industry from a long-range point of view. When a fisherman considers installing a sonar on his boat, however, he is interested in obtaining information for immediate use. Moreover, he is primarily interested in an inexpensive method of efficiently locating fish. Other information is of secondary importance. For the CTFM sonar to be widely accepted in the fishing industry, therefore, it must be inexpensive and its effectiveness as a fish finder needs to be demonstrated.

The sonar model here discussed costs US $210,000. It is much more complex than would be required for fish finding purposes.

The low detection rate for skipjack tuna in the Hawaiian fishery does not mean the CTFM sonar will not be useful as a fish finder in other fisheries. The detection rate for a given species depends on species-related parameters. In most cases, the rate can be expected to be higher than that for skipjack tuna. Because of the importance of the swim bladder in reflecting acoustic energy (Cushing and Richardson, 1955; and Harden Jones and Pearce, 1958) echoes from skipjack tuna, which do not have swim bladders, are weaker than those from many species which do have swim bladders. Species which are more concentrated in their distribution than the apparently widely separated schools of skipjack tuna will have a higher detection rate. The probability of detection increases with an increase in the difference between the swimming speed of the fish and the searching speed of the ship. In general, slower swimming fish will be more likely to be encountered than faster swimming fish such as the skipjack tuna. Whether detection rates will be high enough to justify the cost of a CTFM sonar will have to be determined individually for each fishery.

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